Biodiversity in rubber agroforests

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The research for this thesis was carried out in the Community and Conservation Ecology Group at the Centre for Ecological and Evolutionary Studies (CEES) of the University of Groningen and was part of the 'Alternatives to Slash and Burn' programme at the World Agroforestry Centre (ICRAF) in Bogor, Indonesia.
The research was supported by a grant from The Netherlands Organisation for Scientific Research (NWO) in the framework of the NWO/WOTRO programme 'Biodiversity in disturbed ecosystems'.

Layout and figures: Dick Visser
Cover: Dick Visser
Photos: Hendrien Beukema
Printed by: De Marne

ISBN: 978-90-367-6300-4
ISBN: 978-90-367-6299-1 (digital version)

RIJKSUNIVERSITEIT GRONINGEN

Biodiversity in rubber agroforests

Proefschrift

ter verkrijging van het doctoraat in de
Wiskunde en Natuurwetenschappen
aan de Rijksuniversiteit Groningen
op gezag van de
Rector Magnificus, dr. E. Sterken,
in het openbaar te verdedigen op
vrijdag 1 november 2013
om 12.45 uur

door

Hendrien Beukema

geboren op 5 oktober 1965
te Groningen

Promotores:	Prof. dr. J. van Andel Prof. dr. M.J.A. Werger
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Chapter 1

Introduction

1.1 The problem

Lowland rain forest biodiversity in Sumatra is lost by rapid, large-scale conversion of lowland forest to monoculture plantations. Smallholder agroforestry systems are seen by some as a possible refuge for lowland rain forest species, but little is known about their potential and limitations to contribute to biodiversity conservation. This thesis is an assessment of the role of rubber agroforests in the conservation of lowland rain forest species in Sumatra.

1.2 Deforestation in Sumatra

The island of Sumatra has a total land area of 44.7 million ha (Margono *et al.* 2012). As late as 1900, Sumatra was almost completely covered by forest. MacKinnon (1997) estimates an original forest cover of 99.2% for all of Indonesia, which for Sumatra would amount to a total forest cover of around 44.3 million ha. Deforestation and land use change have drastically reduced forest cover (Jepson *et al.* 2001, Hansen *et al.* 2009). Estimated forest cover was less than 37.4 million ha in 1950 (FWI/GFW 2002, based on Hannibal 1950), 23.3 million ha in 1985 (FWI/GFW 2002, based on RePPProT 1990), 21 million ha in 1990 (Margono *et al.* 2012), 16.6 million ha in 1997 (Holmes 2000, 2002), 15.7 million ha in 2000 (Margono *et al.* 2012), and 13.6 million ha in 2010 (Margono *et al.* 2012). Lowland peneplain forest used to cover about a third of the total Sumatran land area. Holmes (2000) assumed a lowland forest cover of 16 million ha in Sumatra in 1900, and estimated lowland forest cover in 1985 and 1997 to be 5.6 and 2.2 million ha respectively (see Figure 1.1).

Lowland forests in Sumatra were cleared before upland forests and swamp forests because they were the most easily accessible to be cleared for other land uses, and the most profitable for logging. Lowland forest is also the most biologically diverse forest type in Sumatra (Laumonier 1997), and it is different from hill and mountain forest and swamp forest both in the species that inhabit it and in forest structure and ecology. Lowland rain forest now only exists in Sumatra in small fragments and degraded remnants. A similar deforestation process is ongoing in Kalimantan, an area of 53.6 million ha where lowland forest also used to cover about a third of the land.

1.3 Land use change in the Sumatran lowlands

Land use change concentrated along rivers and roads occurred over the last hundred years when local smallholders changed swidden practices to incorporate agroforests and plantations, mostly rubber. The much larger lowland areas between major rivers, originally covered by primary forest, changed more rapidly with the start of large-scale logging operations in the 1970s. Almost all lowland forests have since been logged, and most have now been converted to other land uses, mainly monoculture plantations of oil palm,

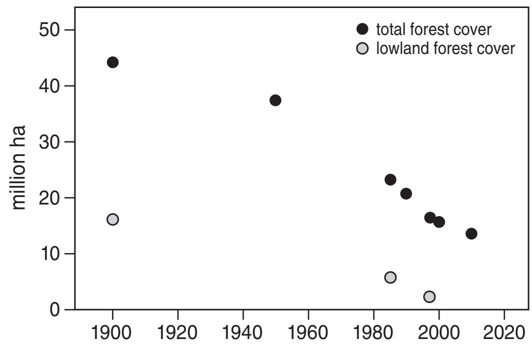

Figure 1.1 Estimated forest cover for the 1900–2010 period in Sumatra in millions of ha, as compiled from different sources (see text).

pulp wood trees, and rubber (Hansen *et al.* 2009). Large monoculture plantations were established mostly by government and private companies, often from outside Sumatra, in large-scale operations. Some of these projects involved participation of transmigrants or local farmers. Conservation of lowland forest biodiversity in sufficiently large protected areas in Sumatra has not occurred. In Jambi province, areas designated as protected forest are not situated in the lowlands. They consist of hill forest (Gunung Tigapuluh and Gunung Duabelas protected areas), swamp forest (Berbak National Park), or hill and mountain forest (Kerinci Seblat National Park) (Potter and Lee 1998).

Smallholder rubber agroforests, also called jungle rubber agroforests, are planted mainly in the lowlands and hills (<500 m altitude). These agroforests are a mixture of rubber trees and other trees, both planted and emerging spontaneously. Jungle rubber agroforests are established after slash-and-burn and have an important wild vegetation component, which make them structurally resemble secondary forests. In the absence of substantial areas of natural lowland forest, those rubber agroforests may currently be fulfilling an unintentional role as a refuge for lowland biodiversity, while being maintained by farmers for the purpose of production only.

1.4 Research problem

The central research question of this study was:
Can a smallholder agroforestry system such as jungle rubber play a role in biodiversity conservation? More specifically, the following four research questions were addressed:

1. What and how much biodiversity is present in jungle rubber, as compared to lowland forest and to monoculture plantations?
2. How can this be assessed and evaluated?
3. What are the limitations of jungle rubber in contributing to biodiversity conservation?
4. Is jungle rubber itself a sustainable land use?

The biological research presented in this thesis addresses mainly the first two questions, and part of the third question, whereas farmer interviews and literature study provide answers to the third and fourth questions as well as the context necessary to translate the biological field results into policy options.

1.5 Research approach

Biodiversity is generally defined as variability at the genetic, species and ecosystem levels (UNEP 1994). In this thesis, biodiversity is regarded in the context of conservation at the ecosystem level. The global community values lowland rain forest as a natural ecosystem that is worth preserving, as expressed by the Convention on Biodiversity to which Indonesia is a signatory. In light of the loss of most of the lowland rain forest that has occurred in Sumatra, the biodiversity that we are interested in conserving at this point in time is lowland rain forest biodiversity. The conservation value of jungle rubber in the lowlands of Sumatra is thus defined in this research by its capacity to provide a suitable environment for viable populations of lowland rain forest species from the same area.

To fully assess this capacity we would have to sample all major taxa of flora and associated fauna, but this is not practically feasible in a highly diverse ecosystem. Instead, pteridophytes were chosen as an indicator group. Pteridophytes occur both in undisturbed forest and in disturbed forest types, and are a relatively well-known group both taxonomically and ecologically. A wide range of terrestrial and epiphytic species occur in the area, and grouping of species based on ecological requirements as described in the literature, such as light conditions and preferred habitat, is possible for this group, so that ‘forest species’ and ‘non-forest species’ could be distinguished. As pteridophytes do not require pollinators and are wind-dispersed, there are few obstacles for establishment of pteridophyte species in a rubber plot after slash-and-burn. The occurrence and abundance of ‘forest species’ and ‘non-forest species’ of pteridophytes may also indicate to what extent jungle rubber provides a forest-like environment that may potentially harbor other groups of forest species. Whether jungle rubber agroforests indeed act as a refuge for other groups of forest species may be limited by hunting pressure (e.g. mammals, birds) or dispersal mechanisms (e.g. trees). Existing datasets on bird and tree diversity were analyzed in the context of this study, and compared to the newly collected pteridophyte data.

Forest and monoculture rubber plantations were included in the sampling to provide reference systems for biodiversity and rubber production values. Jungle rubber combines modest production value for the farmer with an unknown but probably intermediate biodiversity value for the global community, whereas forest and monoculture rubber plantations are on either end of the biodiversity and production scales.

From the outset, it is recognised that jungle rubber as a vegetation type cannot be expected to be highly similar to lowland rain forest. Jungle rubber is established after slash-and-burn, whereas fire is not a frequently occurring natural factor in the tropical rain forest of Sumatra. In addition, the vegetation is partly planted, and dominated by the non-native rubber tree (*Hevea brasiliensis*). The part of the vegetation in jungle rubber that is wild and has spontaneously established consists entirely of successional vegetation, whereas in lowland rain forest successional vegetation is only part of the forest dynamics. It is temporarily present in certain areas in the forest such as tree fall gaps, which are an important part of the forest ecosystem but do not dominate the vegetation as a whole.

To address the successional character of the vegetation in jungle rubber and the length of the planting cycle as potentially important limitations for biodiversity conservation, the age of sampled jungle rubber agroforests was an important factor in the analyses of the biological field data. In addition, limitations of the jungle rubber system related to its primary function of rubber production and to management decisions by the farmer were researched by semi-structured interviews. Jungle rubber is primarily a production system planted and maintained to provide income to owners and tappers. Decisions concerning management intensity, replanting, conversion to other treecrops or to plantation-style rubber production are made by the owner of the rubber agroforest. External factors such as land availability and profitability of jungle rubber influence those decisions and the dynamics and sustainability of the system. Those factors are addressed both by the interviews and by literature study.

1.6 Research area

The peneplain of Jambi province provided a suitable research area as it has relatively uniform environmental conditions. Laumonier *et al.* (2010) delineated eco-floristic sectors for Sumatra as relatively homogenous units in terms of physiography, climate and tree flora composition, representing potential forest types in the absence of human activity. Our research area was located within the sector called *Jambi - Musi to Kwantan <150 m* (Laumonier *et al.* 2010, p. 1159, Fig. 2) where the original forest consisted of lowland Dipterocarp forest (Laumonier 1997). Forest loss in this sector was 71% between 1985 and 2007 (Laumonier *et al.* 2010). Floristically the nonswamp lowland forests in Jambi are similar to those in bordering Riau and South Sumatra (Laumonier *et al.* 2010, p. 1158, Fig. 1). Forest loss in these sectors between 1985 and 2007 was 89% and 74% respectively (Laumonier *et al.* 2010). Smallholder farming in the Jambi peneplain is dominated by rubber agroforests (Levang *et al.* 1999). There were also rubber plantations in the same area for comparison. A map of the study area is included in Chapter 2.

1.7 Outline of the thesis

Chapter 2 describes characteristics of the jungle rubber system, its history and dynamics. It addresses traits of the system related to production that may pose limitations to biodiversity conservation. It also addresses the issue of sustainability of the jungle rubber system itself. It is based on interviews with farmers and on literature study.

Chapter 3 compares and evaluates species richness of terrestrial pteridophytes in forest, jungle rubber and rubber plantations using species-area curves. An independent grouping based on the literature is used to distinguish 'forest species' and 'non-forest species' of terrestrial pteridophytes.

Chapter 4 focuses on individual species to analyse the occurrence of terrestrial pteridophyte species in time during secondary forest succession in jungle rubber. It shows modeled abundance patterns of species that were classified in the previous chapter as 'forest species' or 'non-forest species' based on the literature, and discusses possible indicator species.

Chapter 5 compares the species richness of pteridophytes in forest, jungle rubber, and rubber plantations to that of other plant groups and of birds. Issues important to biodiversity assessment such as scale and species identity are analysed.

Chapter 6 is an analysis and evaluation of the occurrence and reproductive status of epiphytic pteridophytes on trees in forest, jungle rubber, and rubber plantations. Logistic regression is used to assess the importance of land use type, tree type (rubber or other) and tree size for epiphytic pteridophytes.

Chapter 7 is a synthesis. It reflects on the research questions, summarizes the results, and explores future perspectives.

References

FWI/GFW, 2002. The State of the Forest: Indonesia. Bogor, Indonesia: Forest Watch Indonesia, and Washington DC: Global Forest Watch.

Hannibal, L.W., 1950. Vegetation Map of Indonesia. Planning Department, Forest Service, Jakarta. In: Forest Policies in Indonesia: The Sustainable Development of Forest Lands. Jakarta, Indonesia: International Institute for Environment and Development and Government of Indonesia. 1985. Volume 3, Ch. 4.

Hansen, M.C., Stehman, S.V., Potapov, P.V., Arunarwati, B., Stolle, F., Pittman, K., 2009. Quantifying changes in the rates of forest clearing in Indonesia from 1990 to 2005 using remotely sensed data sets. Environ. Res. Lett. 4, 1-12 (034001).

Holmes, D., 2000. Deforestation in Indonesia: A View of the Situation in 1999. Jakarta, Indonesia: World Bank. Draft Report of July 3.

Holmes, D.A., 2002. The predicted extinction of lowland forests in Indonesia. Pages 7-13 in E. Wickramanayake, E. Dinerstein, C.J. Loucks, D.M. Olson, J. Morrison, J. Lamoreux, M. McKnight, and P. Hedao, editors. Terrestrial ecoregions of the Indo-Pacific: a conservation assessment. Island Press, Washington, D.C.

Jepson, P., Jarvie, J.K., MacKinnon, K., Monk, K.A., 2001. The end for Indonesia's lowland forests? Science 292, 859-861.

Laumonier, Y., 1997. The vegetation and physiography of Sumatra. Geobotany 22. Dordrecht, Kluwer.

Laumonier, Y., Uryu, Y., Stüwe, M., Budiman, A., Setiabudi, B., Hadian, O., 2010. Eco-floristic sectors and deforestation threats in Sumatra: identifying new conservation area network priorities for ecosystem-based land use planning. Biodiversity and Conservation 19, 1153-1174.

Levang, P., Yoza, B.K., Tasman, A., 1999. In the shadow of rubber. Alternative agricultural development perspectives in Jambi. Jakarta, IRD and Departemen Transmigrasi dan PPH, Jambi Regional Development Project (World Bank).

MacKinnon, J., ed. 1997. Protected Areas Systems Review of the Indo-Malayan Realm. Canterbury, UK: Asian Bureau for Conservation.

Margono, B.A., Turubanova, S., Zhuravleva, I., Potapov, P.V., Tyukavina, A., Baccini, A., Goetz, S., Hansen, M.C., 2012. Mapping and monitoring deforestation and forest degradation in Sumatra (Indonesia) using Landsat time series data sets from 1990 to 2010. Environ. Res. Lett. 7, 1-16 (034010).

Potter, L.M., Lee, J., 1998. Tree planting in Indonesia: Trends, impacts and directions. CIFOR Occasional Paper 18. Bogor, Indonesia.

RePPProT (Regional Physical Planning Programme for Transmigration), 1990. The Land Resources of Indonesia: A National Overview. Final report. Land Resources Department of the Overseas Development Administration, London (Government of UK), and Ministry of Transmigration (Government of Indonesia), Jakarta, Indonesia.

UNEP, 1994. Convention on biological diversity. Text and annexes. Interim Secretariat for the Convention on Biological Diversity, Geneva, Switzerland.

Chapter 2

Jungle rubber system

Hendrien Beukema

2.1 Introduction

On the island of Sumatra, much rubber is produced in what looks like native forest to an outsider, despite the fact that the rubber tree came from Brazil and was introduced as a plantation tree about a century ago. The rubber cultivation system described as 'jungle rubber' (Gouyon *et al.* 1993) combines planting of these non-native rubber trees, after slash-and-burn, with minimal interference in the growth of natural successional forest vegetation. The resulting agroforest structurally resembles a multi-layered secondary forest, with many tree species other than rubber.

The forest vegetation around the rubber trees in a jungle rubber agroforest provides some important ecological services to the farmer. It helps to shade out weeds, thus reducing the workload for the farmer and making the plot less prone to fire. It also helps to retain moisture, which is especially important in very dry periods such as El Niño events. According to farmers, it also keeps temperatures a bit lower which is good for latex flow when the trees are tapped in the early morning. Last but not least, jungle rubber agroforests have an additional economic function as a source of timber, firewood, and fruits and vegetables that are either planted or have established themselves spontaneously.

A by-product of the jungle rubber system happens to be that these agroforests provide habitat for some of the plants and animals of the natural forest whose natural habitat is rapidly disappearing in Sumatra. But since biodiversity conservation as such is not on the farmer's agenda (De Foresta and Michon 1992), we need to understand the evolution and dynamics of the system from a farmer's perspective in order to understand how the biodiversity within it might be faring in the long term.

This chapter describes the evolution, characteristics, and dynamics of jungle rubber based on a literature study and on interviews with farmers. Since jungle rubber agroforests are privately owned, decisions concerning planting and management are made by the owner and family members. This chapter identifies decisions by farmers that may affect biodiversity, and explores the driving forces behind those decisions.

2.2 The beginnings of jungle rubber: literature on the 1890s to the 1930s

2.2.1 From gathering to cultivating, and from Ficus to Hevea

In the 19th century Jambi had little economic development, and infrastructure was poorly developed. The province was still largely covered by natural forest, and transport was mainly by river, the important river systems running West to East in the direction of Jambi town, shipping port to the trade centre of Singapore on the opposite shore.

Most people practiced shifting cultivation and the gathering of forest products. Latex (getah) from various local forest trees was an important component of those forest products. It became more important at the end of the 19th century, when demand from the industrialized countries for natural rubber created a 'rubber boom' and exports rose (Purwanto 1993). Stimulated by high prices, farmers and colonial officials became interested in cultivating latex-producing trees as a more productive alternative to gathering latex in the forest. High prices stimulated the change from gathering to cultivating. The change was needed because the high demand for the product led to unsustainable overexploitation of forest trees and the breakdown of traditional tenure systems (Dove 1994). Planting trees provided for a higher production capacity by increasing the number of tappable trees and by selecting species that could be tapped far more often than most of the latex-producing trees growing in the wild.

The first plantations were established in the 1890s using a local species: *Ficus elastica* (Purwanto 1996). Although 'para rubber' (*Hevea brasiliensis*, a species from the Amazon) was already known in Indonesia at that time, *F. elastica* was preferred initially as it gave higher yields in field trials. It was only after a new way of tapping of *H. brasiliensis* trees was developed in Malaysia during the last decade of the 19th century that para rubber reached higher yields and became the favored species for planting (Van Gogh 1938, Barlow 1978).

One of the reasons for the success of Hevea rubber with local farmers and its rapid expansion in planted area was that it fitted smoothly into existing practices, both of the cultivation system and of the trading system (Anonymous/W.W.v.R. 1924, Pelzer 1978). The land clearing by slash-and-burn practiced by shifting cultivators allowed for planting of *H. brasiliensis* together with the rice and other crops in the first few years of the cycle. River transport to Jambi town was easy by locally made rafts, and the (mainly Chinese) trade channels for export to Singapore were already in place (Van Gelder 1950).

2.2.2 Early rubber production systems

We can distinguish two main influences shaping the early production systems of planted Hevea rubber in Jambi: **(i)** an influence from outside, introducing plantation management practices jointly with the introduction of *Hevea* as a new and exotic tree crop, and **(ii)** an influence from inside: the existing practices of shifting cultivation and gathering of forest products that the local population in Jambi was familiar with.

(i) Hevea plantations were developed earlier on the Malaysian peninsula than in Jambi, and the introduction of *Hevea brasiliensis* to farmers in Jambi was to a large extent from Malaysia because of existing trade and ethnic relations, migrant plantation workers and passing pilgrims (haji's) (Van Gelder 1950). The first substantial rubber plantations in Malaysia were established around 1896, and by 1905 the area under rubber had already expanded to 18,600 ha (Barlow 1978), mainly owned by European planters. At the beginning of the 20th century, many local farmers from Central Sumatra went to work on the new rubber plantations in Malaysia, to avoid taxes and corvee labor introduced by the recently established Dutch control in Central Sumatra, and attracted by high wages (Anonymous/W.W.v.R. 1924). Many later returned to Jambi bringing *Hevea* planting material (seeds and seedlings) and experience from working on the plantations. Broersma (1926) noted that many smallholders copied the art of rubber cultivation from large-scale, mainly European-owned, plantations. Those plantations were clean-weeded and planted with the best selected planting material known at the time.

(ii) In Jambi, the first smallholder rubber was planted in 1904, as reported in 1918 by the agricultural extension officer W.A. Zegers Rijser (Tideman and Sigar 1938). He reported a different type of rubber cultivation: rubber trees were growing in a wilderness of shrubs and trees. This cultivation system incorporated aspects of existing practices of both shifting cultivation and the gathering of forest products. In shifting cultivation, plots were left alone after one or two years of rice cultivation, when soil fertility decreased (Van Breda de Haan 1916). Any useful trees planted in those first years after slash-and-burn were left to grow, and were visited later to collect products such as fruits. Rubber trees were an addition to this system. Large numbers of rubber seedlings or seeds were planted with food crops in the first years after slash-and-burn, and then the plot was left. In the dense, quickly growing secondary vegetation that followed food crop cultivation, many of the rubber seedlings did not survive, but the ones that did could be tapped after about 10 years. Before the introduction of *Hevea*, the available time after the rice harvest was spent on the collection of forest products, while after the introduction of *Hevea* this time was spent on tapping of rubber trees (Van Breda de Haan 1916). The tapping of rubber trees resembled the collection of forest products in the sense that the rubber trees were growing in a (secondary) forest, surrounded by natural forest vegetation. The rubber trees could be far apart, but tappers knew where to find them. In other words, farmers applied practices that they were familiar with to cultivate the new tree crop.

Rubber proved to be very well adapted to this kind of growing conditions (Pelzer 1978). Although the growth was a bit slower in this system, the regeneration of the bark after tapping seemed better than in clean plantations (Cumming 1924, Cumming and Pekelharing 1925). In the early days of smallholder rubber, some farmers grew rubber under a plantation-type of management, but only near towns where suitable land was scarce. The majority cultivated what is today called jungle rubber (Anonymous/W.W.v.R. 1924).

Some colonial officers and planters were critical of the way local people cultivated rubber, accusing them of a lack of care for the trees and wondering whether locals were at all able to cultivate tree crops. Moreover, they argued that the unweeded jungle rubber would become a source of pests and weeds that could harm their carefully managed plantations (Broersma 1926). These misgivings were at least partly inspired by the growing fear of competition from local rubber farmers, a fear that grew rapidly as the area of jungle rubber quickly expanded and prices were expected to fall because of overproduction. Local people could produce much more cheaply than colonial estates that had to make up for their investments (Broersma 1926).

The farmer's labor input for land clearing and weeding during the first few years was required for the cultivation of rice and other crops, and planting rubber did not require much additional labor investment (Van Gelder 1950). Planting material became available for free or at very low cost after rubber trees in Jambi started to bear fruit, allowing the farmer to plant rubber at high densities. This reduced the need for further weeding as troublesome weeds such as alang-alang (*Imperata cylindrica*) were outshaded by a quickly closing canopy. The high planting density also allowed for mortality of rubber seedlings resulting from competition with secondary forest vegetation. In the years before tapping, the dense secondary vegetation helped to keep out wild animals such as pig and tapir, that damaged the young rubber. In the productive phase, the forest-like vegetation created a cool environment conducive of a good latex flow. Of course, the production per hectare and the quality of the latex were lower than those of the estates, but inputs were low as well and farmers could quickly expand their area planted with jungle rubber, which they did. Van Breda de Haan (1916) mentions the increased prosperity of the local population resulting from their high earnings from Hevea rubber, which he saw as one of the causes of a reported increase in the imports of foreign rice to Jambi.

The colonial planters became aware of the ecological rationality and economic flexibility of the jungle rubber system, and worried that local people would be in a better position to handle falling prices.

2.2.3 Response to price fluctuations in the absence of diversification (1920s and 1930s)

During most of the 1920s, the rubber price was high. This was partly due to the Stevenson's restriction scheme limiting rubber exports (Knorr 1945). This scheme was an effort put in place by the British government to stabilize fluctuating rubber prices by putting limits on the tonnage of rubber that could be exported. The Netherlands' Indies, however, didn't take part in this restriction scheme, but profited from it through an increase in exports and market share. Until 1929, the local population made large profits from their rubber (Touwen 1991, Purwanto 1993). High prices stimulated rubber planting, and while initially there was no labor shortage for tapping, when the tappable area expanded much more labor was needed. Tappers were hired from other parts of Sumatra (especially from Kerinci) and later from Java. A side effect of the success of rubber in Jambi province was a lack of interest to invest in crop diversification.

When prices collapsed in the 1930s due to the world economical crisis, the expectation was that below a certain price the farmers would stop tapping altogether. This was not the case, because other export crops were never really developed in Jambi and farmers had no possibility to change to another crop (Broersma 1926), because they needed the money to supplement insufficient local rice production. Inputs were minimized and the hired tappers were sent home, but the owner and his family took up or continued rubber tapping. They increased tapping frequency as a strategy to earn more by increasing the output (Touwen 1991, Dove 1993). Planting also continued since it was little extra effort to incorporate rubber seeds or seedlings in the slash-and-burn patches for rice production, and seeds were now available freely in reproductive rubber plots. An added advantage of rubber planting was that in local (adat) law, planting trees on a plot of land could create ownership rights (Dove 1993).

From these historical developments it is clear that in the absence of diversification the farmer reacted to both high and low prices by tapping and planting rubber. It is likely that large areas of mature jungle rubber planted in the 1920s remained untapped later on because of the lack of labor (Van Gelder 1950). Despite higher outputs, farmers' incomes were lower due to low rubber prices, making local rice production again a priority, and this further increased labor shortages for tapping rubber.

2.3 Current characteristics and trends

The jungle rubber system as described in the early literature is still in use (Gouyon *et al.* 1993), but cannot be expected to be exactly the same as in the early days of rubber cultivation. To better understand the dynamics and assess the sustainability of the jungle rubber system, interviews were carried out with owners and tappers of productive rubber plots and with owners who were in the process of (re)planting rubber. Interviews focused on changes within the jungle rubber system, especially those that could affect biodiversity, as well as on changes away from jungle rubber systems. One big change in recent times has been the much wider availability of improved planting material such as high-yielding clonal planting material and clonal seedlings. These improved planting materials have been present in Jambi for a long time (Beery 1956), but adoption has been limited (Gouyon 1999). Wider adoption of those planting materials could lead to a shift towards more plantation-style rubber systems. Another big change has been the change in land use in general, with large oil palm and timber plantation projects providing more options for converting old jungle rubber plots.

Two series of interviews with Jambi farmers were held, the first in June–July 1998 and the second in December 1999. Both were in the same location: villages in the lowlands of Jambi province, roughly between Jambi town in the East and the foothills of the Barisan mountain range in the West. The methodology of these two interview series is presented in Box 2.1, and the locations of the research villages in Figure 2.1 and Table 2.1. Analysis of the interview results has led to the following observations.

2.3.1 Land holdings and land use

Owners of the biodiversity research plots were asked about their land and land use. Owners of biodiversity research plots that were jungle rubber plots had between 4.8 and 92.8 ha of land in ownership, the median value was 14.6 ha (N = 18), see Table 2.2. Most farmers owned more than one rubber plot, usually in a variety of stages, from immature to past productive. Productive rubber plots were tapped regularly, while unproductive rubber plots included immature rubber, mature rubber that could be tapped but was not tapped at the time of the research, or over-age rubber that was not productive any longer. Farmers owned between 1 and 45 ha of productive rubber plots, with a median value of 3 ha.

Though rubber is the main crop in Jambi (Levang *et al.* 1999, Wibawa *et al.* 2000), most farmers do not solely rely on rubber (see Table 2.2). For Jambi farmers, income is usually related to having sufficient rice to feed the family. Rice can be grown, or bought with the revenue from other crops. Lowland rice cultivation (sawah) is the most productive form of rice cultivation, but it is not as common in the Jambi lowlands as it is in other parts of Indonesia, because of lack of suitable terrain. There are villages that have no lowland rice cultivation at all, and they rely solely on (less productive) upland rice, and rice bought on the market with revenue from cash crops such as rubber. Upland rice (ladang) is cultivated both in swiddens (Van Noordwijk *et al.* 2008), without rubber, and as part of rubber cultivation during the first and second year after slash-and-burn.

Box 2.1 Methodology of interviews with farmers

The criteria for selection of farmers to be interviewed and the questions asked were not the same for both series of interviews. Therefore each series will be discussed separately below.

Description of the interviews held in 1998 (biodiversity research plots)
Productive, regularly tapped rubber plots of different ages and management intensities were selected for biodiversity research in the 1996–1998 period (this thesis): 23 jungle rubber plots and 17 rubber plantation plots. The age of the plots ranged from 5 to 74 years old, each age class was represented by a few plots. The owners and some of the tappers of those plots were interviewed by the author and a local assistant.

Of the total of 40 plots, 35 belonged to farmers of which 34 were interviewed. The remaining 5 were part of large-scale rubber plantations owned by a state company ('inti' of PTP Nusantara VI); interviews for those were done with company staff.

Of the 35 plots owned by farmers, 5 were part of a large plantation scheme ('plasma' of PTP Nusantara VI), 7 plots were privately owned plantations, while 23 plots were of a jungle rubber type and privately owned. For the 23 jungle rubber plots, 21 interviews were obtained: one owner of a jungle rubber plot could not be interviewed, and one interview covered two plots in the same 10 ha agroforest.

Questions were asked about the land holdings of the farmer and about the history, management and production of the rubber plot. In addition the farmer's opinion was asked about perceived problems in rubber cultivation and future developments in land use in his area. The interviews took about 1.5 hour per farmer. Apart from the owner it was sometimes necessary to interview other informants as well, for instance a previous owner, a family member or a sharetapper, especially in the case of very old plots or absentee owners. In some instances not all of the questions were answered.

Description of the interviews held in 1999 (newly planted plots)
The criteria for selecting rubber plot owners to be interviewed were very different from the 1998 series of interviews. In this case, farmers who recently planted new rubber or were in the process of planting were selected. The target was 4 to 6 farmers per village who had been planting rubber during the last three years (1997 to 1999 period) or were ready for planting in 2000. If farmers replanting rubber were not found, farmers clearing other types of land such as secondary vegetation or forest land were interviewed instead.

A total of 62 plots spread over 14 out of the original 16 research villages were identified as being cleared by slash-and-burn in the 1997–1999 period, and farmers were interviewed about those plots by teams of local assistants. Of the 62 newly planted plots, 60 plots were indeed planted with rubber as expected, while 2 plots were actually planted with oil palm (*Elaeis guineensis*) and areca nut (*Areca catechu*), respectively.

With regard to plot history, 38 of the 62 plots were previously used for rubber cultivation, while 24 plots were derived from other vegetation types. Of the 38 plots that were previously used for rubber cultivation, 37 plots were previously jungle rubber plots, and 1 plot was previously a rubber plantation. Of the 37 plots that were previously jungle rubber plots, 12 plots were still productive jungle rubber plots just before they were replanted, while the other 25 were not productive any longer.

The interview consisted of 2 parts: the first part dealing with the (re)planting process and the second with the previous jungle rubber plot or rubber plantation that was replanted. In the first part questions were asked about the slash-and-burn process and the new rubber planted. In the second part of the interview questions were asked about the history and the past management and production of the rubber plot that was replanted. In both parts questions were asked about the land situation of the (previous) owner. For the first part, data on all of the 62 selected plots was collected. For the second part, only 30 farmers (out of 38 with replanted rubber plots) could be interviewed, many of whom did not answer all of the questions.

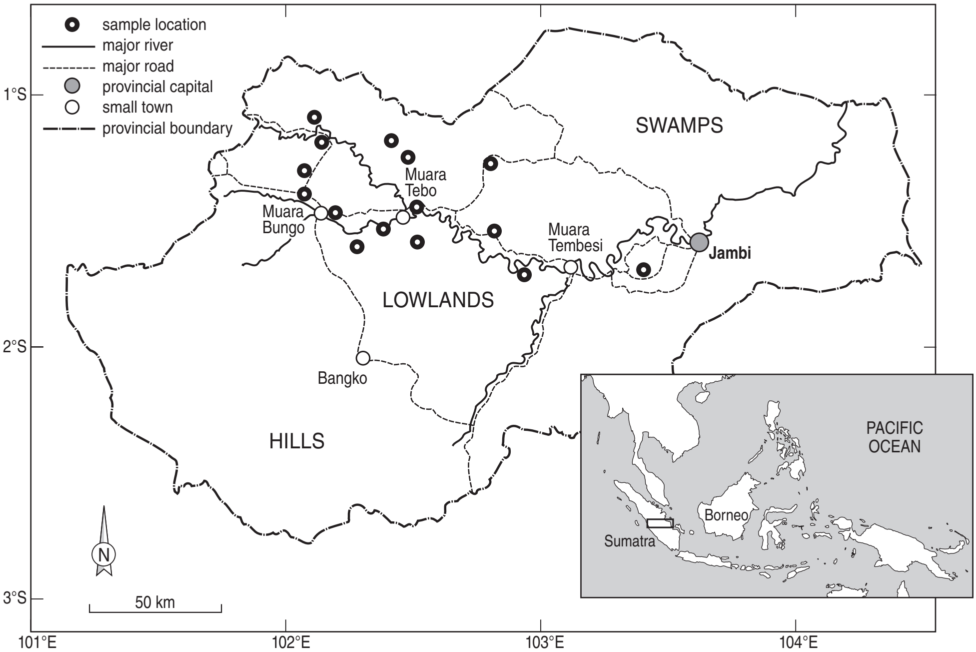

Figure 2.1 Locations of the biodiversity research plots in the lowland area of Jambi province, Sumatra.

Table 2.1 Villages in Jambi province, Sumatra, where the biodiversity research plots are located. Interviews about the biodiversity research plots (productive jungle rubber and rubber plantation plots) were held in these villages. In addition, interviews were held in 14 of the 16 villages with farmers who had just planted, or were in the process of planting, a new plot.

Village (desa)	Subdistrict (kecamatan)	District (kabupaten)
Sarana Jaya	Muara Bungo	Bungo Tebo
Wiroto Agung	PWK Rimbo Bujang	Bungo Tebo
Dusun Tuo Ulu	PWK VII Koto	Bungo Tebo
Teluk Cempako	PWK VII Koto	Bungo Tebo
Balai Rajo	Tebo Ulu	Bungo Tebo
Rejo Sari	Muara Bungo	Bungo Tebo
Muara Kuamang	PWK Pelepat	Bungo Tebo
Sungai Bungur	Tebo Tengah	Bungo Tebo
Sungai Tilan	Tebo Tengah	Bungo Tebo
Semabu	Tebo Tengah	Bungo Tebo
Muara Sekalo	PWK Sumay	Bungo Tebo
Semambu	PWK Sumay	Bungo Tebo
Lubuk Kambing	PWK Merlung	Tanjung Jabung
Sungai Puar	Mersam	Batang Hari
Batin	Muara Bulian	Batang Hari
Maro Sebo	Jambi Luar Kota	Batang Hari

Table 2.2 Use of land owned by 18 owners of jungle rubber plots, in hectares.

Prod. rubber	Unprod. rubber	Lowland rice	Upland rice	Shrub land	Fruit trees	House lot and yard	Other	Total ha
4.5			0.25			0.03		4.78
1				3.5	15 trees	0.04	1 ha pasture, 0.25 ha garden crops	5.79
2	5							7
3						0.5	4 ha pasture	7.5
3	3			3	0.36	0.01		9.37
3	5			1		0.06	1 ha sengon, 1 fish pond	10.06
1.5	7.5	0.5				0.03	2 ha pasture	11.53
2	10							12
3		1		10	40 trees	0.002	2 fish ponds	14.002
2	6	2		2		0.25	1 ha sengon, 2 ha garden crops	15.25
8	3.2		2			1	2 ha oil palm	16.2
5	5		3	5		0.02		18.02
1	7	1	1	8	0.25	0.01	2 ha barren land	20.26
20			1	5		0.5	1 ha alang-alang grass, 4 fish ponds	27.5
4	4	4		20	2	0.08		34.08
4	17	0.5	1	6			2 ha coffee, 10 ha cinnamon	40.5
45	5	10	1	4	508 trees	0.08	8 ha barren land, 4 ha pasture, 2 ha garden crops	79.08
20	40	0.75		30	1	1		92.75

Shrub land (belukar) can have different origins, but is often part of swiddening, or it can be a failed rubber plot where not enough rubber trees survived. Alang-alang grass (*Imperata cylindrica*) is not favored by farmers as it is very susceptible to fire (Van Gelder 1950, Gouyon *et al.* 1993), but areas with this grass can be converted to other land uses (De Foresta and Michon 1996). Crops that are alternatives to rubber and are sold to buyers outside the village and local markets include fruits, cinnamon, oil palm, and sengon (*Paraserianthes falcataria*), a fast-growing tree used for timber and pulp.

Owners of the rubber plantation plots had between 2 and 190.8 ha of land in ownership, the median value was 12.05 ha (N = 11), see Table 2.3. These farmers owned between 2 and 40 ha of productive rubber plots, with a median value of 4 ha.

Table 2.3 Use of land owned by 11 owners of rubber plantation plots, in hectares.

Prod. rubber	Unprod. rubber	Lowland rice	Upland rice	Shrub land	Fruit trees	House lot and yard	Other	Total ha
2								2
2.5								2.5
2						0.05	0.95 ha sengon	3
5				0.25				5.25
2	4	0.75		2	55 trees	0.005		8.755
6			0.6	3		0.45	2 ha alang-alang grass	12.05
17				1		0.09		18.09
8	6.5	1		3	0.25		1 ha garden crops	19.75
3	7			6		0.02	4 ha garden crops	20.02
4	23				1	0.5	1 ha alang-alang grass	29.5
40	140	10			0.5	0.25		190.75

2.3.2 Labor

Owners of jungle rubber agroforests and rubber plantations often deal with labor shortages because rubber is part of a larger farming system that has seasonal peaks in labor, e.g. rice planting and harvesting. Establishing a new rubber plot is also a major labor and time investment.

If the owner has more rubber than can be tapped by the family, or in case of an absentee owner, a tapper is hired (Wibawa *et al.* 2000). Tappers will usually receive a share of the yield, or receive wages from the owner. Of the 23 jungle rubber research plots, 18 (78%) were tapped by a tapper who was not the owner, while only 5 were tapped by (the family of) the owner (22%). Of the 12 privately owned rubber plantation plots, half were tapped by a tapper and half by (the family of) the owner.

Sometimes it can be difficult for an owner to find a tapper when there is other work offered in the area. It is fairly common that a productive rubber plot is not tapped for some period of time. Of 22 jungle rubber plots, 12 (55%) experienced such 'resting periods'. Most of these plots would not be tapped for a few weeks to a few months every year because labor was needed elsewhere, while some would not be tapped for half a year to a year, or in one case even three years, because a tapper could not be found. Resting periods can increase the productive life span of a rubber tree, as it allows for bark regeneration. Of the 12 privately owned rubber plantations, only one plantation had a resting period of 6 months, while the other plantations were tapped regularly without interruptions.

2.3.3 Rubber plot sizes

The biodiversity research plots were all productive rubber plots. The jungle rubber plots in this group ranged in size from 0.25 to 10 ha, with a median size of 1.5 ha (N = 21), while the rubber plantations ranged in size from 0.5 to 35 ha, with a median size of 2.3 ha (N = 12). The owners of these plots were asked about the sizes of any other rubber plots they had. This way, information on the size of 11 additional jungle rubber plots was collected. Those ranged in size from 0.5 ha to 4 ha, with a median size of 1.5 ha. Information was also collected on the size of 9 additional rubber plantation plots (both clonal rubber and clonal seedlings). Those ranged in size from 1.5 ha to 3 ha, with a median size of 2 ha.

Of the 62 newly planted plots, only 13 had been rubber plots that were still productive just before they were replanted. Of those, 12 were jungle rubber plots that ranged in size from 0.75 to 8 ha, with a median size of 1.75 ha, and 1 was a rubber plantation of 0.75 ha. Of the newly planted plots that were planted with rubber (N = 60), those planted with unimproved ('wild') planting material ranged in size from 0.4 to 3.5 ha with a median size of 1.5 ha (N = 16), those planted with clonal seedlings ranged in size from 0.5 to 3 ha with a median size of 1.25 ha (N = 25), and those planted with clonal planting material ranged in size from 0.75 to 8 ha with a median size of 1.5 ha (N = 19).

2.3.4 Secondary products from jungle rubber agroforests

Mature jungle rubber agroforests are a mix of rubber trees and other trees. Some of the useful non-timber species have grown spontaneously in the agroforest (Gouyon *et al.* 1993), while others were planted together with the rubber. Yields of secondary products such as fruits are not high, but they provide diversity in family nutrition and are valued as such.

In the biodiversity research plots, 20 out of 22 jungle rubber plots had planted non-timber trees other than rubber, such as fruit trees. The average number of species planted was 6 (N = 20), with an average density of 50 trees per hectare (N = 17). Non-timber species that were considered useful and had grown spontaneously were present in 19 out of 20 jungle rubber plots, the average number of species was 4 (N = 19) and the density was 29 trees (or clumps, e.g. bamboo) per hectare (N = 17).

Of the 12 privately owned rubber plantations, 7 had planted trees other than rubber; here also the average number of species planted was 6 species. The average density was 26 trees per ha in 6 plots, while 1 plot had 446 planted trees per ha. Of the privately owned rubber plantations, 5 plantations had an average of 2 useful species that had grown spontaneously, with a density of 5 trees (or clumps) per ha (N = 4).

Some of the trees that grow spontaneously in jungle rubber agroforests are timber trees, which can be used for construction of (temporary) housing, to build fences to keep destructive wild animals (mainly pigs) away, and for firewood. Wood can be taken out as needed while the rubber plot is still productive. In the biodiversity research plots, wood was taken out of 9 of the 23 productive jungle rubber plots. In three of the latter plots, some forest trees had been left standing during field preparation for rubber planting, because they were too big to fell without the use of a chain saw. Rubber plantation plots did not have any timber species. Both jungle rubber and rubber plantation plots provided firewood, in the form of old rubber trees that had stopped producing.

When rubber plots are (re)planted, the wood of the cut vegetation is often used for building temporary housing, for fencing the new plot, and/or for income to offset part of the cost of land preparation for replanting. Farmers were asked about the use of the wood at the time of planting.

Of the biodiversity research plots, only 2 out of 22 owners of jungle rubber plots (planted between 1923 and 1989) constructed a fence around their new plots, while owners of 4 out of 14 rubber plantation plots (planted between 1979 and 1993) did so. Of the biodiversity research plots, 4 plots had been jungle rubber plots before they were (re)planted in the 1988–1993 period. During land preparation for replanting, wood from 3 of these plots was used by the owner (both timber species and rubber wood). The reason given for not selling any of the wood was that there was no buyer.

For the newly planted plots (planted 1997–2000), information about the construction of a fence was obtained for 52 of the 60 plots that were planted with rubber. Only 1 out of 16 plots planted with 'wild' planting material was fenced, while 7 out of 23 plots planted with clonal seedlings were fenced, and 8 out of 13 plots planted with clonal planting material were fenced.

Of the 62 newly planted plots, 37 had been jungle rubber plots before replanting. During land preparation for replanting (1997–2000), wood from these plots was sold in a few cases (4 plots, or 11%, of which timber species were sold from 3 plots and rubber wood from 1 plot). Owners mentioned four reasons for not selling any of the wood: they used it themselves (22 plots, or 59%), there was no useful wood in the plot (3 plots, or 8%), they preferred to burn it (7 plots, or 19%), or there was no buyer (1 plot, or 3%).

2.3.5 The age of jungle rubber

Because rubber needs to grow at least 5 years before it becomes productive, and can normally be tapped for at least 15 years, the planting cycle is theoretically 20 years or more. Jungle rubber however can get much older than that. In Jambi, plantation rubber, which has an economic lifetime of 20 to 25 years, is cut after 20 years or less, but jungle rubber older than 25 years is very common. The long planting cycle of jungle rubber is important for smallholders because of the cost and risks (e.g. pests, fire) involved in establishing a new rubber plot.

Data was collected on the expected cycle length of the biodiversity research plots by asking about the year of planting and the expected year of replanting for these plots. Farmers were also asked about the year the rubber trees were first tapped, to calculate the unproductive period before the plots started producing, as well as the expected productive period.

For jungle rubber plots of less than 20 years old, the expected cycle length ranged from 24 to 65 years, with a median length of 37 years and an average length of 44 years (N = 6). (When older plots were included, the expected cycle length ranged from 24 to 76 years, with a median length of 48 years and an average length of 50 years (N = 20)). The length of the unproductive period, before the trees were tapped, varied in time (see

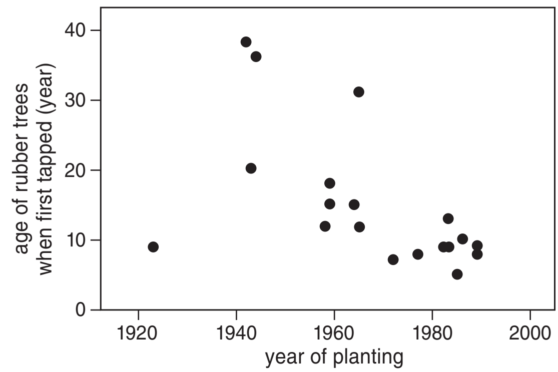

Figure 2.2 Length of unproductive period of jungle rubber plots (N = 20), by planting year.

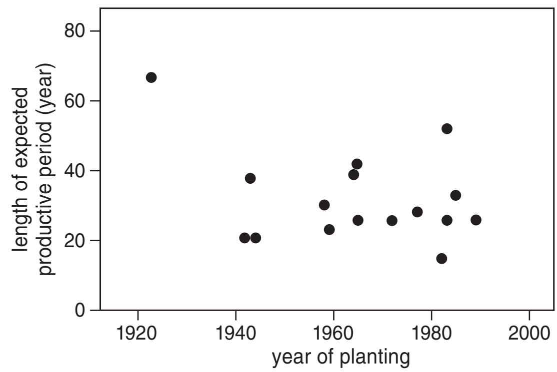

Figure 2.3 Length of expected productive period of jungle rubber plots (N = 17), by planting year.

Figure 2.2). The oldest plot, planted in 1923, was first tapped at 9 years old. Some of the plots planted in the 1940–1970 period remained untapped for long after the trees matured, while for plots planted in the 1970–1990 period, tapping usually started when the rubber trees were about 9 years old. The expected productive period however was similar for plots planted in the 1940–1970 and 1970–1990 periods (see Figure 2.3), and unrelated to the length of the unproductive period.

All jungle rubber plots were planted with unimproved planting materials from seeds collected in other jungle rubber agroforests. Those unimproved planting materials (seeds and seedlings) are called 'wild' ('liar' in Indonesian).

Of the rubber plantation plots, 5 were planted with clonal seedlings. This planting material originates from the seeds and seedlings of clonal rubber trees in plantations planted with clonal material. Clonal seedlings are uncertified but are regarded improved planting material in the sense that trees are supposedly more productive (Gouyon *et al.* 1993). The expected cycle length for plantations of clonal seedlings ranged from 24 to 41 years, with a median length of 25 years and an average length of 29 years (N = 4). On average, tapping started after 6 years, and the expected productive period was 23 years. The other 12 plantation plots were planted with improved planting material, mostly the GT1 clone. The expected cycle length for clonal plantations ranged from 19 to 32 years, with a median length of 21 years and an average length of 23 years (N = 8). On average, tapping started after 6 years, and the expected productive period was 17 years.

Of the 62 newly planted plots, the 12 plots that were jungle rubber and still productive just before they were replanted ranged in age from 19 to 79 years old. The median age was 43 years and the average was 45 years old (N = 12). A total of 25 of the 62 replanted plots were jungle rubber plots that were not productive any longer at the time of replanting. Those ranged in age from 20 to 79 years old. The median age was 47 years and the average was 45 years old (N = 24). There was also one plot that had been a rubber plantation that was still productive just before it was replanted. This rubber plantation plot was 15 years old when it was replanted.

2.3.6 Production of jungle rubber

Jungle rubber agroforests are estimated to have an average yearly production of about 500 kg of dry rubber per ha (Budiman and Penot 1997). It turned out to be difficult to collect production figures for individual rubber plots in the scope of this study. Only some of the owners and tappers that were interviewed were systematically keeping track of the production of individual plots. Farmers who did keep an administration did not always write down the weight of the weekly production (slab rubber), but sometimes noted an amount of money received from a transaction. Rubber is usually traded weekly at the village level in a system involving middle men, who often double as lenders and suppliers of consumption goods, and who control the price (Wibawa *et al.* 2000). This makes it difficult to translate the amount of money received back to the weight of the rubber slabs involved in the transaction. For this reason, the number of rubber trees per hectare was used to stand in for production of the rubber plots in this study. Owners and tappers generally know how many trees are tapped, as well as the size of their plots.

In both series of interviews, farmers were asked about the number of rubber trees in their plots. The results were converted to rubber trees per hectare and plotted as two data series in Figure 2.4. While there is overlap between the data, replanting was limited to plots of 19 years and older, containing 200 trees per hectare or less.

2.3.7 Replanting

When forest land is available, farmers tend to prefer clearing (primary and secondary) forest land rather than old rubber plots for planting of new rubber. This is because the planting of rubber trees provides a claim to the land (Gouyon *et al.* 1993, Suyanto *et al.* 2001), and because plots established on former (primary) forest land have fewer weed problems (Van Gelder 1950, Gouyon *et al.* 1993, Suyanto *et al.* 2001).

Of the 31 biodiversity research plots of which the land use history could be recorded, 27 (87%) were forest (primary, logged, or secondary forest) before they were planted with rubber. The 4 plots (13%) that were previously planted with jungle rubber were all replanted in the 1989–1993 period, which was the most recent period included in this research.

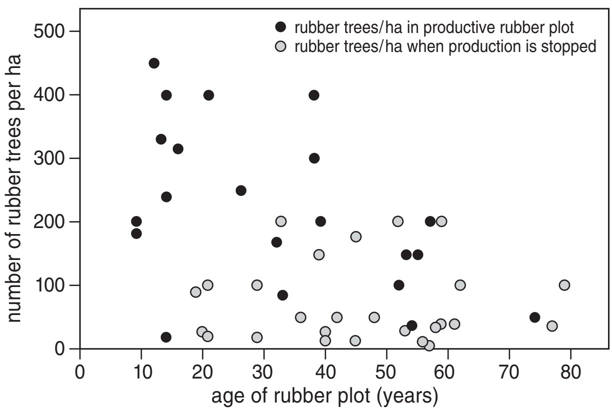

Figure 2.4 Number of rubber trees in productive vs. replanted rubber plots of different age. Filled dots: productive rubber trees in the biodiversity research plots. Grey dots: productive rubber trees in plots just before replanting.

Of the 62 newly planted plots, planted in the 1997–2000 period, only 21 (34%) were forest (primary, logged, or secondary forest) before they were planted, while 25 (40%) were jungle rubber plots that were not productive anymore, 12 (19%) were productive jungle rubber plots, 1 (2%) was a productive rubber plantation, and 3 (5%) were failed plantations (2 rubber plots and 1 cinnamon plot where too many trees died in the first few years after planting). Of the 25 jungle rubber plots that were not productive anymore, data was collected for 14 of them with regard to the post-productive period before they were replanted. Those 14 plots had been unproductive for 1 to 19 years, with a median of 7 years and an average of 8.4 years.

Table 2.4 Cost per hectare associated with planting rubber, by planting material used ('wild', clonal seedlings, clonal). Cost of acquiring land and labor cost not included. Currency: Indonesian Rupiah (1999).

	'Wild' (N = 16)	**Clonal seedlings** (N = 23)	**Clonal material** (N = 13)
slash-and-burn	70,461.31	125,657.00	292,820.51
fence	37,500.00	139,666.67	245,651.28
temporary housing	-	48,913.04	269,230.77
planting material	4,878.95	59,283.57	521,174.36
herbicides	-	31,416.67	162,294.87
fertilizers	-	15,521.74	60,000.00
planting	7,276.79	-	23,076.92
manual weeding	28,630.95	7,826.09	11,384.62
materials	-	40,869.57	67,512.82
total cost per ha	**148,748.00**	**469,154.35**	**1,653,146.15**

Of the newly planted plots that were planted with rubber (N = 60), 16 were planted with 'wild' planting material, 25 with clonal seedlings, and 19 with clonal planting material. Of these plots, 6 were part of a project that provided clonal planting material for free, and 2 were part of a project that provided clonal seedlings for free, while 52 plots were planted privately without the assistance of a project. Farmers were asked about the cost associated with planting for these 52 plots, see Table 2.4. Plots were grouped by the planting material used. Clonal seedlings are more expensive than 'wild' planting material, and clonal material is more expensive than clonal seedlings. The table shows that farmers using more expensive planting material also invested more in other aspects of planting. Plots planted with clonal seedlings usually yield about 750 kg/ha, and with clonal material about 1500 kg/ha per year, versus 500 kg/ha for 'wild' planting material (Gouyon 1999).

2.4 Potential factors affecting biodiversity

The extent to which jungle rubber agroforests may function as a refuge for forest species may be affected directly by farmers' decisions regarding (i) the length of the planting cycle, (ii) the way the rubber is managed, and (iii) the use of wood, and indirectly by (iv) changes in the landscape matrix and (v) land use diversification.

2.4.1 Cycle length

A long cycle length is supposed to affect biodiversity in a positive way. One would expect the oldest jungle rubber to be replanted first, but results from the interviews regarding the age of the jungle rubber when it was replanted span a wide range of ages. This might indicate that other factors such as production may be more important than age in the decision to replant. These are family-level decisions: how does a jungle rubber plot feature in the context of family income and investment, is family labor available, and what other options are there in terms of other crops or other pieces of land to cultivate? Often the decision to replant is a matter of timing with regard to the productivity and labor requirements of other plots that the family owns.

In productive jungle rubber plots, owners and tappers take care of spontaneous rubber seedlings by removing vines and small trees around seedlings so they can grow freely. Some farmers also do supplemental planting of seedlings, both in the early pre-productive phase if not enough of the initial seedlings survived, and later on when the plot is already productive. As the plot gets older, these additional spontaneous or planted seedlings grow into tappable rubber trees, creating a mixed-aged stand (Gouyon 1996). What contributes to a long cycle length, positively affecting biodiversity, is this growth of spontaneous rubber seedlings inside the agroforest to form a multigenerational stand, as well as long pre-productive and post-productive periods.

It seems, however, that long pre-productive periods are no longer common, as rubber trees are taken into production earlier. Long post-productive periods may also disappear as old jungle rubber is among the first land targeted for oil palm and timber projects that are planned to include village land. Jungle rubber is also increasingly replanted, though this is a relatively recent phenomenon. Though many farmers own areas of secondary vegetation that could be planted with rubber, replanting of old jungle rubber plots is becoming more common. One reason may be that primary and logged-over forests, which are preferred for establishing new rubber plots (Gouyon *et al.* 1993), have become scarce (Gouyon 1999). For replanting, old jungle rubber plots may be preferred over younger secondary vegetation (aged 6 years, Suyanto *et al.* 2001, to at most 15–20 years, Gouyon 1999) because of a lower risk of weeds such as *Imperata*, or because some of the secondary vegetation is set aside for slash-and-burn cultivation of upland rice.

Economic development, including off-farm labor opportunities, may bring more available capital for investment in replanting. This may affect both the cycle length, as the lack of capital is often a major reason to delay replanting, as well as the type of management of the new rubber plot.

2.4.2 Management

Although farmers feel that a 'clean plantation' is the norm, and many indicate that they would like to own such a plantation if they had the money to invest (or they could take part in a project), they are very well aware of the rationality of the minimal-input system that jungle rubber is, and value the added advantages of low labor requirement and additional products. Rather than an inevitable shift for all rubber production towards plantation style management, it may well be that the distinct systems can coexist in the landscape to meet a range of needs and strategies.

The style of management of rubber plots seems to be related to the planting material used. On one end is a low-input system using 'wild' planting material gathered for free or at low cost that goes with minimal inputs overall, a strategy that requires little capital investment and results in jungle rubber agroforests. On the other end is a rubber plantation system using expensive clonal material, that goes with high investments overall and application of the 'estate package' of using herbicides and fertilizers.

The use of clonal seedlings seems to result in a kind of intermediate between the two in terms of investment, production, and cycle length. However in terms of management, the productive rubber plots planted with clonal seedlings observed in the field resembled plantations rather than jungle rubber agroforests. They were mostly rubber monocultures with a few useful trees mixed in, most of those planted, and lacking the spontaneous secondary forest vegetation component of jungle rubber agroforests. This is not to say that rubber plots that were planted with clonal seedlings more recently will necessarily resemble plantations. Given the increased availability and adoption of clonal seedlings as planting material, and the perception by farmers that these seedlings are 'stronger' than the more expensive clonal material, it is possible that clonal seedlings are being used to replace 'wild' planting material in a jungle rubber system that is slightly more productive, but otherwise not much changed in terms of management.

Budiman and Penot (1997) argue that farmers are gradually adopting some of the components of the 'estate package'. They mention the use of clonal seedlings, planting in rows to facilitate tapping, application of one selective weeding per year in pre-productive rubber (first tapping possible after 6–7 years instead of 8–10 years), intercropping, and control of *Imperata* by herbicides. One could also argue that those changes represent merely small tweaks of the pre-productive phase of the jungle rubber system, requiring relatively little additional capital and labor investment. If the weeding is selective, meaning that useful vegetation is spared, such rubber plots may well resemble old-style jungle rubber agroforests as they get older, the main difference being the fact that rubber trees are planted in lines.

The 'jungle rubber' and 'estate package' strategies are very different in terms of investment and management intensity; they seem to represent a clear choice for one system or another, rather than a gradual change (Williams *et al.* 2001). The only jungle rubber element that can be found in privately owned rubber plantations is the planting of a few fruit trees and other useful trees, which is an element of jungle rubber that is valued and incorporated when the switch to a plantation style is made.

In terms of potential for biodiversity conservation, there is a vast difference between the two systems. Once the choice is made to invest in expensive planting material, the 'estate package' management style means that there is no tolerance for any spontaneous regrowth (Williams *et al.* 2001). The resulting 'clean' plantation does not have any secondary forest vegetation that could support associated biodiversity.

According to Gouyon (1999), "the cost to bring one hectare of clonal plantation to maturity is Rp 7.5 million. Of this, half is labor costs, much of it to control weeds. Clones grown with no maintenance and no fertilizer – as is jungle rubber – have poor growth and production and give insufficient return to match the initial investment in the planting material." This is confirmed by the belief of farmers that clones are not 'strong' and will die without pampering. Clonal seedlings are generally favored by farmers as they promise higher production while being 'strong'. As such, they may increase yields while maintaining the jungle rubber management style.

2.4.3 The use of wood
The rise in demand for wood could mean that timber trees in old jungle rubber plots are more valued than before. This would increase the value and attractiveness of jungle rubber as a multi-product system (De Foresta and Michon 1992). On the other hand it could also mean that more trees will be harvested during the lifetime of the agroforests, which would have a negative effect on biodiversity. Increased sale of rubber wood (Gouyon 1999) could provide more capital when rubber is replanted, and may thus stimulate replanting and investment in the new plot.

2.4.4 The landscape matrix
Jungle rubber agroforests, traditionally situated in bands along transportation routes like rivers and roads, used to be arranged along the edges of large core areas of lowland rain forest. Typically, rubber plots would be found at walking distance in a band of a few kilometers around a village, and further along the river where it could be reached by boat. More inland, beyond the rubber area, one would reach the forest. With large-scale deforestation (Ekadinata and Vincent 2011), most jungle rubber areas are no longer embedded in a forest matrix. This greatly reduces the source populations for biodiversity in the agroforests.

2.4.5 Land use diversification

From an economic point of view, the conversion of forest lands to other land uses presents more options for farmers to choose different crops, to have their land included in projects, and to have alternative employment possibilities. Although rubber is still the main source of income for most farmers in the Jambi lowlands, some diversification has taken place, especially with the development of other plantation crops such as oil palm and fast growing trees for timber and pulp (Sofiyuddin *et al.* 2012). Improved infrastructure means better access to markets for such products as fruits and timber (Gouyon 1996), which could be grown either in a jungle rubber setting or more intensively in mixed or monoculture plantations.

Expansion of the jungle rubber area, on the other hand, seems to have become very limited in most areas. A historical abundance of available forest land has been replaced by large-scale plantations (Ekadinata and Vincent 2011), increasing conflicts (Suyanto 2007) and limiting villagers to already cultivated land. In addition, the tradition of expanding jungle rubber holdings through establishment of new villages by the younger generation has come to a halt, as existing villages cannot freely use surrounding forest land anymore because of a limitation of their land rights (Gouyon 1999).

The indirect effects of this land use differentiation on biodiversity in rubber production systems are still largely unknown. In this study, I focus on investigating the effects of management options within these systems.

2.5 Perspective

Our surveys indicated that jungle rubber was still being planted and grown, though a shorter life cycle can be expected for this rubber. Otherwise, the basic characteristics of jungle rubber did not seem to have changed much since its introduction. The strategy of minimizing inputs is still a sensible option for many farmers, if only for part of their rubber holdings. At the landscape level however there seems to be a change away from jungle rubber systems and towards plantation style cultivation (Ekadinata and Vincent 2011), making jungle rubber a less common feature in the landscape.

In the following chapters the results of ecological research into biodiversity aspects of the jungle rubber system are presented. This research was carried out in the 'biodiversity research plots' mentioned in this chapter (first series of interviews), which included 23 jungle rubber plots and 17 rubber plantation plots. Effects of cycle length and management intensity on selected indicator groups of species were studied by comparing jungle rubber and rubber plantations of different age to each other and to old growth forest plots that served as a baseline reference. The Synthesis (Chapter 7) reflects on the impact of management factors touched upon in this survey, considers aspects of ecological and economical sustainability of the different systems, and evaluates the role of jungle rubber systems as a refuge for lowland rainforest species.

References

Anonymus (W.W.v.R.). 1924. De bevolkingsrubber cultuur. Nederlandsch-Indisch Rubber- en Thee-Tijdschrift 9, 246–249.

Barlow, C. 1978. The natural rubber industry: its development, technology and economy in Malaysia. Kuala Lumpur, Oxford University Press.

Beery, L.A. 1956. Smallholder rubber in Indonesia. Report, International Cooperation Administration.

Broersma, R. 1926. De Indonesiër met zijn rubber. Koloniaal Tijdschrift 2, 146-165.

Budiman, A.F.S., and E. Penot. 1997. Smallholder rubber agroforestry in Indonesia. Paper presented at the International Rubber Conference 1997, Kuala Lumpur, 6-9 October 1997. Bogor, Indonesia, Gapkindo / ICRAF S.E. Asia.

Cumming, T.J. 1924. Report on a visit to the residency of Djambi (Netherlands East Indies). Federated Malay States Government Press, Kuala Lumpur.

Cumming, T.J., and N.R. Pekelharing. 1925. De bevolkingsrubber in Djambi. De Indische Culturen (Teysmannia) Proefnummer: 53–59.

De Foresta, H., and G. Michon. 1992. Complex agroforestry systems and conservation of biological diversity (II). Pages 488–500 in Yap Son Kheong and Lee Su Win, eds. Proceedings of the International Conference on Tropical Biodiversity 'In Harmony with Nature' 12–16 June 1990. Kuala Lumpur, Malaysia.

De Foresta, H., and G. Michon. 1996. The agroforest alternative to *Imperata* grasslands: when smallholder agriculture and forestry reach sustainability. Agroforestry Systems 36 (1–3), 105-120.

Dove, M.R. 1993. Smallholder rubber and swidden agriculture in Borneo: a sustainable adaptation to the ecology and economy of the tropical forest. Economic Botany 47, 136–147.

Dove, M.R. 1994. Transition from native forest rubbers to *Hevea brasiliensis* (Euphorbiaceae) among tribal smallholders in Borneo. Economic Botany 48, 382–396.

Ekadinata, A. and G. Vincent. 2011. Rubber agroforests in a changing landscape: analysis of land use/cover trajectories in Bungo district, Indonesia. Forests, Trees and Livelihoods 20, 3–14.

Gouyon, A. 1996. Ecological and socio-economic conditions of rubber agroforestry in the Dipterocarp ecosystems of Indonesia. Pages 369-388 in A. Schulte and D. Schöne, eds. Dipterocarp forest ecosystems: towards sustainable management. World Scientific Publ., Singapore.

Gouyon, A. 1999. The sustainable development of tree crops and the prevention of vegetation fires in South Sumatra, Indonesia. Jungle rubber. Report, European Union and Ministry of Forestry and Estate Crops, Forest fire prevention and control project. Kanwil Kehutanan dan Perkebunan, Palembang.

Gouyon, A., De Foresta, H., and P. Levang. 1993. Does 'jungle rubber' deserve its name? An analysis of rubber agroforestry systems in southeast Sumatra. Agroforestry Systems 22, 181–206.

Knorr, K.E. 1945. Rubber and its regulation. Food Research Institute, Stanford University Press, California.

Levang, P., Yoza, B.K., and A. Tasman. 1999. In the shadow of rubber. Alternative agricultural development perspectives in Jambi. Report, Jambi Regional Development Project (World Bank). IRD and Departemen Transmigrasi dan PPH, Jakarta.

Pelzer, K.J. 1978. Swidden cultivation in Southeast Asia: historical, ecological, and economic perspectives. Pages 271–286 in P. Kunstadter, E.C. Chapman and S. Sabhasri, eds. Farmers in the forest. Economic development and marginal agriculture in Northern Thailand. University Press of Hawaii, Honolulu.

Purwanto, B. 1993. The economy of the native population in Southern Sumatra between 1850 and 1910. Review of Indonesian and Malaysian Affairs 27[1-2], 106–133.

Purwanto, B. 1996. The economy of Indonesian smallholder rubber, 1890s-1940. Verhandelingen der Koninklijke Nederlandse Akademie van Wetenschappen 167, 175–192.

Sofiyuddin, M., Rahmanulloh, A. and S. Suyanto. 2012. Assessment of profitability of land use systems in Tanjung Jabung Barat District, Jambi Province, Indonesia. Open Journal of Forestry 2(4), 252–256.

Suyanto, S. 2007. Underlying cause of fire: Different form of land tenure conflicts in Sumatra. Mitigation and Adaptation Strategies for Global Change 12(1), 67–74.

Suyanto, S., Tomich, T.P., and K. Otsuka. 2001. Land tenure and farm management efficiency: The case of smallholder rubber production in customary land areas of Sumatra. Agroforestry Systems 52 (2), 145–160.

Tideman, J., and P.F.L. Sigar. 1938. Djambi. Serie samenvattende overzichten van gewestelijke gegevens No. 1. Mededeeling No. XLII, Koninklijke Vereeniging "Koloniaal Instituut", Amsterdam.

Touwen, L.J. 1991. Voordeel van veelzijdigheid; de economische ontwikkeling van Palembang en Djambi tussen 1900 en 1940. Economisch- en Sociaal-historisch Jaarboek 54,134–182. Nederlandsch Economisch-Historisch Archief, Amsterdam.

Van Breda de Haan, J. 1916. De rijstteelt in de laaglanden der residentie Djambi. Tijdschrift voor het Binnenlandsch Bestuur 51, 259–276.

Van Gelder, A. 1950. Bevolkingsrubbercultuur. Pages 427–475 in C.J.J. van Hall and C. van de Koppel, eds. De landbouw in de Indische Archipel. Deel III. Uitgeverij W. van Hoeve, Den Haag.

Van Gogh, F. 1938. Het ontstaan en de groei van de ondernemings- en de bevolkingsrubbercultuur in Nederlandsch-Indië. Economisch Weekblad voor Nederlandsch-Indië 7, 125–129.

Van Noordwijk, M., Mulyoutami, E., Sakuntaladewi, N., Agus, F. 2008. Swiddens in transition: shifted perceptions on shifting cultivators in Indonesia. Occasional Paper no.9. Bogor, Indonesia: World Agroforestry Centre.

Wibawa, G., Hendratno, S., Rosyid, M.J., Budiman, A., and M. Van Noordwijk. 2000. The role of socio-economic factors in farmer decision making. Progress Report. IRRI Sembawa Research Station / ICRAF S.E. Asia, Indonesia.

Williams, S.E., Van Noordwijk, M., Penot, E., Healey, J.R., Sinclair, F.L., and G. Wibawa. 2001. On-farm evaluation of the establishment of clonal rubber in multistrata agroforests in Jambi, Indonesia. Agroforestry Systems 53, 227–237.

Chapter 3

Terrestrial pteridophytes as indicators of a forest-like environment in rubber production systems in the lowlands of Jambi, Sumatra

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Published in Agriculture, Ecosystems & Environment 104 (2004), 63-73.

Abstract

Species richness of terrestrial ferns and fern allies (Pteridophyta) may indicate forest habitat quality, as analysed here for a tropical lowland area in Sumatra. A total of 51 standard 0.16 ha plots in primary forest, rubber (*Hevea brasiliensis*) agroforests and rubber plantations was compared for plot level diversity (average number of species per plot) and landscape level diversity (species–area curves). Average plot level species richness (11 species) was not significantly different amongst the three land use types. However at the landscape level the species–area curve for rubber agroforests (also called jungle rubber) had a significantly higher slope parameter than the curve for rubber plantations, indicating higher beta diversity in jungle rubber as compared to rubber plantations. Plot level species richness is thus not fully indicative of the (relative) richness of a land use type at the landscape scale because scaling relations differ between land use types. Terrestrial fern species can serve as indicators of disturbance or forest quality as many species show clear habitat differentiation with regard to light conditions and/or humidity. To assess forest habitat quality in rubber production systems as compared to primary forest, terrestrial pteridophyte species were grouped according to their ecological requirements into 'forest species' and 'non-forest species'. Species–area curves based on 'forest species' alone show that the understorey environment of jungle rubber supports intermediate numbers of 'forest species' and is much more forest-like than that of rubber plantations, but less than primary forest. Species richness alone, without *a priori* ecological knowledge of the species involved, did not provide this information. Jungle rubber systems can play a role in conservation of part of the primary rain forest species, especially in areas where the primary forest has already disappeared. In places where primary forest is gone, jungle rubber can conserve part of the primary forest species, but large areas of jungle rubber are needed. In places where primary forest is still present, priority should be given to conservation of remaining primary forest patches.

3.1 Introduction

With the disappearance of undisturbed lowland rain forest habitat the question arises whether disturbed habitat maintains some of the characteristics and functions of the original forest, to what extent it can support survival and reproduction of primary rain forest species and how this function is influenced by management practices. For a complete answer of this question we would have to consider all major taxa of flora and associated fauna. The research reported here compares diversity of terrestrial pteridophyte species, with known habitat requirements, to assess for this group to what extent the understorey habitat in rubber production systems is comparable to the understorey habitat in undisturbed rain forest for the lowland peneplain of Jambi (Sumatra).

3.1.1 Exploratory research and remaining questions

De Foresta and co-workers were probably the first to study the vegetation of rubber agroforests (also called 'jungle rubber'; Gouyon *et al.*, 1993) to get an impression of species richness. Sampling a 100 m transect line (Michon and De Foresta, 1995) they found almost twice as many herb species in a rubber agroforest as compared to a nearby primary forest (23 versus 12 species) in Jambi province, Sumatra. Their research was broad in the sense that all vegetation was included, but limited in the fact that vegetation types were represented by a 100 m transect only and that the study was not replicated across the landscape. When a larger number of plots are sampled, will the average number of herb species per plot remain twice as high for jungle rubber as compared to primary forest? Another question that remained after the exploratory work by Michon and De Foresta was whether high diversity found on the plot level is a reflection of high species turnover (beta diversity) on a landscape scale, or not. Data on plot level have been used (Leakey, 1999) to make statements that 'complex, multistrata agroforests contain about 70% of all the regional pool of plant species', apparently assuming that a single transect line is sufficient to characterise a vegetation type and that scaling rules above plot level do not differ between vegetation types.

3.1.2 Species turnover and species composition

In spite of a high number of species found at the plot level, if the species composition in jungle rubber at the landscape level would be rather repetitive, in other words if the species–area curve for jungle rubber would have a much lower slope parameter than the curve for primary forest, those rubber agroforests would probably not be as interesting an option for biodiversity conservation.

Species richness, regardless of species composition, is often used as a measure in biodiversity studies. If we deal with disturbed ecosystems however, there are risks involved because different taxa react in different ways to disturbance. For many taxa, "diversities peak at intermediate rates of small-scale disturbance" (Rosenzweig, 1995, p. 39). Although species are considered the 'currency' of biodiversity, counting just any species does not help us much when we are interested in conservation of a specific ecosystem. What kind of species do we find? Do the species we find give us some information about the quality of the type of habitat we are interested in? The fact that we can find great diversity of pteridophyte species on the forest floor of rubber agroforests does not tell us that the environment there is comparable to a primary forest and can be expected to support primary forest species.

3.1.3 Terrestrial pteridophytes as an indicator group

For assessments using an indicator group we should know first of all whether the group of species we are using contains enough species that differ in habitat requirements with respect to the range of the environmental factors that change when a forest is disturbed by human action. If the great majority of pteridophyte species were generalist species that could grow anywhere they would not indicate any changes in forest environment due to disturbance. Enough species with narrow habitat requirements are needed so they can be grouped to indicate different degrees of disturbance. Important environmental factors for life in the understorey of a tropical lowland rain forest that change with disturbance are light conditions (quantity and spectrum) and microclimate (moisture and temperature regime). When species are thus grouped we can assess which part of the total diversity in each land use type is made up by species requiring forest-like conditions, assuming that the bigger the share of those 'forest species', the more forest-like the understorey environment will tend to be.

3.1.4 Research questions

Summarising the above, the research is focussed on the following questions:

- Can rubber production systems play a role in conservation of primary forest species by providing forest-like habitat?
- Can terrestrial pteridophyte species indicate disturbance level or habitat quality of the forest understorey?
- Is plot level species richness indicative of the (relative) richness of a land use type at the landscape scale, or do scaling relations differ essentially between land use types?
- Is species richness a useful indicator of habitat quality, or is (*a priori*) ecological information needed on the species involved?

3.2 Land use change in the Jambi lowlands

The study was carried out in the lowlands of the peneplain area in Jambi province, Sumatra at elevations of 40–150 m above sea level. For sampling locations see Figure 3.1.

The original forests of this area are mixed Dipterocarp rain forests. The physical environment, structure and floristics of these forests and of the derived secondary vegetation types are described by Laumonier (Laumonier, 1997, pp. 88–130). Extensive research on land use and land use changes has been carried out by the 'Alternatives to Slash-and-Burn' project and summarised in two reports (Van Noordwijk *et al.*, 1995 and Tomich *et al.*, 1998). Land use types described by the ASB project (Tomich *et al.*, 1998, Table I.2, p. 19) include natural forest, forest extraction (community-based forest management,

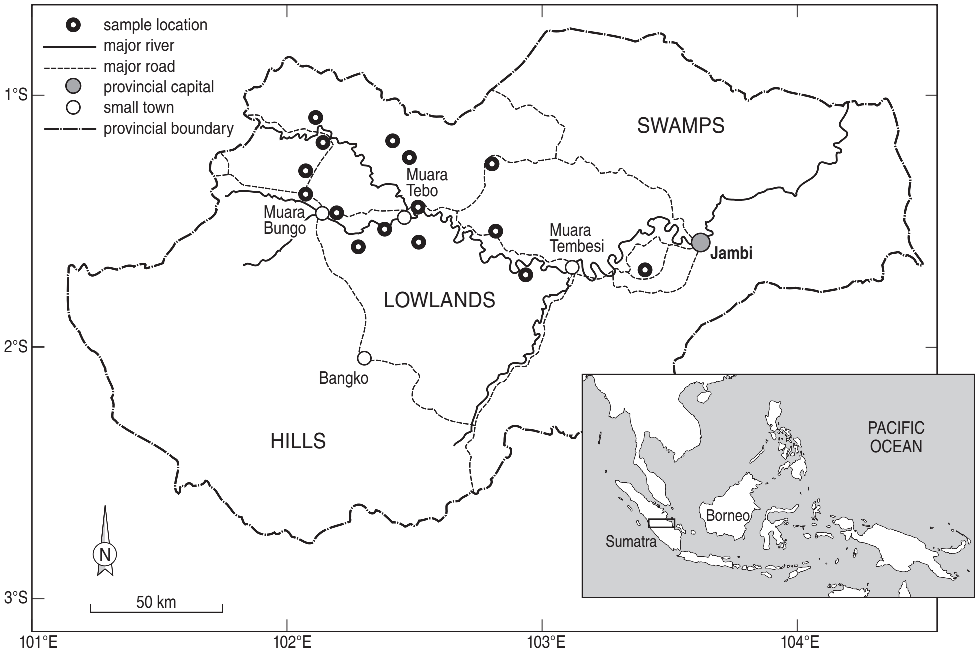

Figure 3.1 Sampling locations in the lowland area of Jambi province, Sumatra.

commercial logging), complex multistrata agroforestry systems (rubber agroforests), simple tree crop systems (rubber, oil palm (*Elaeis guineensis*) and industrial timber monoculture), crop/fallow systems (upland rice (*Oryza sativa*)/bush fallow rotation), continuous annual cropping systems (monoculture cassava degrading to *Imperata cylindrica*), and grasslands/pasture (*I. cylindrica*).

Primary and logged-over forests in the Jambi lowlands are disappearing fast in recent years, they are replaced mainly by plantations (oil palm, rubber, timber) and to a lesser extent by smallholder agroforests (rubber, fruit trees). By the end of the 1990s much of the lowland primary and logged-over forests as shown on Laumonier's 1986 vegetation map (Laumonier, 1997) had already been converted to other land uses (survey by H. Beukema, 1997). Unfortunately an up to date land use map showing these current rapid changes is not available. For generalised maps of land use changes in the Jambi lowlands in the 1980s, see Beukema *et al.* (1997).

3.3 Rubber production systems

In Jambi province rubber is produced mainly in rubber agroforests and to a lesser extent in more intensively managed monocultural plantations. Both production systems use slash-and-burn to clear land before planting.

In the monocultural plantations rubber (latex) is the only product. The undergrowth below the rubber trees is kept low by using herbicides and by manual weeding, while fertilisers are applied around the rubber trees to stimulate their growth. Tapping starts when the rubber trees are 5–6 years old. Trees remain productive until they are 20–25 years old and a new planting cycle starts.

In the jungle rubber production system there are a number of secondary products next to rubber (latex) that is the main product. Rubber is planted together with rice, vegetables, herbs, and a limited number of useful trees such as fruit trees. Weeds are controlled manually and only during the first 2 or 3 years when rice and vegetables are produced. After that the secondary vegetation that comes in naturally and includes useful species is allowed to grow with the rubber. A dense secondary forest vegetation builds up. Around 9 years after planting, a path between the rubber trees is made and tapping starts. Through natural regeneration of rubber seedlings and active replanting in gaps by the farmer (Wibawa *et al.*, in review), those rubber agroforests can remain productive much longer than rubber plantations. A secondary forest dominated by rubber is the result. In an average 'jungle rubber' agroforest only about 40% of trees with a diameter at breast height (DBH) of over 10 cm are rubber trees. The other trees are mostly natural regrowth while some trees are planted by the farmer.

3.4 Method

3.4.1 Plot sampling

Three land use types with associated anthropogenic disturbance levels were sampled: undisturbed rain forest (11 plots), low disturbance jungle rubber (23 plots) and high disturbance rubber plantations (17 plots). The 'undisturbed' rain forest was old growth forest without visible traces of timber cutting and without known history of logging or shifting cultivation, the only human use being limited collection of non-timber forest products and hunting.

Plots were located across the Jambi peneplain, a slightly undulating to flat area of around 200 km × 150 km with rather uniform soils in the centre of Sumatra. The total area of each land use type in the Jambi peneplain is unknown, but the area under jungle rubber is much larger than the area under either rubber plantation or undisturbed forest. In each land use type, the total area sampled is very small compared to the total area of the land use type, so the differences in sampling intensity are probably less important.

Standard plots of 40 m × 40 m (0.16 ha per plot) were subdivided into 16 subplots of 10 m × 10 m each. Counting presence of terrestrial pteridophyte species in the 16 subplots of each plot resulted in a frequency score between 0 and 16 for each species in each plot. For this paper, only presence of species in plots was analysed. Edge effects were avoided by locating the plots away from forest edges and roadsides. Small paths used by rubber tappers however were considered characteristic of jungle rubber systems and therefore not avoided. Plots were located well away from rivers and streams to avoid rheophytes that indicate moisture rather than any level of anthropogenic disturbance.

Only productive rubber systems were sampled. Age of jungle rubber plots varied from 9 to 74 years, while the age of rubber plantation plots was 5–19 years old.

3.4.2 Pteridophyte grouping

Pteridophyte species were grouped based on ecological notes in literature on Malaysian species (Alston, 1937; Backer and Posthumus, 1939; Fletcher and Kirkwood, 1979; Holttum, 1932, 1938, 1959a,b, 1963, 1966, 1974, 1981, 1991; Holttum and Hennipman, 1978; Kramer, 1971; Page, 1976; Pemberton and Ferriter, 1998; Piggot and Piggot, 1988; Spicer *et al.*, 1985; Wong, 1982). From the literature, it became clear that there is enough habitat differentiation among species to make pteridophytes potentially a suitable indicator group for this study. We would have liked to classify our species by their optima for both light and microclimate conditions, but the available species descriptions (mostly from taxonomical literature) included consistent information on light requirements and preferred habitat only. Nevertheless that information was sufficient to classify the species into ecological groups for the purpose of this study. Based on the literature four levels for light conditions were distinguished: 'open' conditions, 'open/light shade', 'light shade' and 'shade/deep shade'. In combination with data on preferred habitat the species were assigned to one of two groups arbitrarily named 'forest species' and 'non-forest species'.

'Forest species' are all species that require shade or deep shade plus the species that require light shade and grow in forest. 'Non-forest species' are all species of open and open/light shade conditions plus the species that require light shade and prefer habitats other than forest (roadsides, forest edges, plantations, etc.). This grouping does not imply that 'non-forest species' never grow in the forest. Some of them do occur in forest, especially in gaps, but they are more abundant in open conditions. Species are thus grouped by (inferred) ecological optimum rather than by ecological range.

Of a total of 65 terrestrial pteridophyte species found in the survey, 36 were classified as 'forest species' and 26 as 'non-forest species' (see Table 3.1). Three species remained unclassified because they were not identified to the species level and could not be linked to literature (Table 3.1). They were excluded from analyses concerning 'forest species'. Although species–area curves are of course sensitive to the removal of species from the data, we expect the effects to be limited in this case. Of the three species that were excluded, two unclassified *Cyathea* species (labelled *Cyathea* sp.2 and *Cyathea* sp.3) were most likely not 'forest species' in our classification and would not have been included in the analysis anyway. They were not encountered in forest at all. *Cyathea* sp.2 occurred more often in rubber plantations than in jungle rubber: it was found in four rubber plantation plots and in one jungle rubber plot (24 and 4% of those plots, respectively) while *Cyathea* sp.3 occurred in one rubber plantation plot and in one jungle rubber plot. Both species were found to be growing more abundantly in the rubber plantation plots than in the jungle rubber plots. The third species that was excluded was an unclassified *Asplenium* species occurring as a single individual in a jungle rubber plot.

3.4.3 Data analysis

For statistical analysis the program SPSS Version 10.0 was used.

Table 3.1 Species list of terrestrial pteridophyte species found in Jambi lowlands, for classification criteria see text.

Family	Species name	Group
Aspleniaceae	*Asplenium glaucophyllum* v.A.v.R.	Non-forest
Aspleniaceae	*Asplenium longissimum* Bl.	Non-forest
Aspleniaceae	*Asplenium pellucidum* Lam.	Forest
Aspleniaceae	*Asplenium* sp.	Not classified
Blechnaceae	*Blechnum finlaysonianum* Hk. & Grev.	Forest
Blechnaceae	*Blechnum orientale* L.	Non-forest
Blechnaceae	*Stenochlaena palustris* (Burm.) Bedd.	Non-forest
Cyatheaceae	*Cyathea* cf. *contaminans* (Hooker) Copel.	Non-forest
Cyatheaceae	*Cyathea moluccana* R. Br.	Forest
Cyatheaceae	*Cyathea* sp.2	Not classified
Cyatheaceae	*Cyathea* sp.3	Not classified
Dennstaedtiaceae	*Lindsaea* cf. *repens* (Bory) Thw.	Forest
Dennstaedtiaceae	*Lindsaea cultrata* (Willd.) Swartz	Forest
Dennstaedtiaceae	*Lindsaea divergens* Hk. & Grev.	Forest
Dennstaedtiaceae	*Lindsaea doryphora* Kramer	Forest
Dennstaedtiaceae	*Lindsaea ensifolia* Swartz	Non-forest
Dennstaedtiaceae	*Lindsaea parasitica* (Roxb. Ex Griffith) Hieron.	Forest
Dennstaedtiaceae	*Microlepia speluncae* (L.) Moore	Non-forest
Dennstaedtiaceae	*Pteridium caudatum* (L.) Maxon subsp. *yarrabense* (Domin) Parris	Non-forest
Dryopteridaceae	*Diplazium crenatoserratum* (Bl.) Moore	Forest
Dryopteridaceae	*Diplazium malaccense* C. Presl	Forest
Dryopteridaceae	*Diplazium pallidum* Bl.	Forest
Dryopteridaceae	*Diplazium riparium* Holtt.	Forest
Dryopteridaceae	*Diplazium tomentosum* Bl.	Forest
Dryopteridaceae	*Pleocnemia irregularis* (C. Presl) Holtt.	Forest
Dryopteridaceae	*Tectaria barberi* (Hk.) Copel.	Forest
Dryopteridaceae	*Tectaria fissa* (Kunze) Holtt.	Forest
Dryopteridaceae	*Tectaria singaporeana* (Wall. ex Hk. & Gr.) Copel.	Forest
Dryopteridaceae	*Tectaria vasta* (Bl.) Copel.	Forest
Gleicheniaceae	*Dicranopteris linearis* (Burm. f.) Underw. var. *linearis*	Non-forest
Gleicheniaceae	*Dicranopteris linearis* (Burm. f.) Underw. var. *subpectinata* (Christ.) Holtt.	Non-forest
Hymenophyllaceae	*Trichomanes javanicum/singaporeanum*	Forest
Hymenophyllaceae	*Trichomanes obscurum* Bl.	Forest
Lomariopsidaceae	*Teratophyllum* cf. *ludens* (Fée) Holtt.	Forest
Lomariopsidaceae	*Teratophyllum* cf. *rotundifoliatum* (R. Bonap.) Holtt.	Forest
Lycopodiaceae	*Lycopodium cernuum* L.	Non-forest
Nephrolepidaceae	*Nephrolepis biserrata* (Sw.) Schott	Non-forest
Ophioglossaceae	*Helminthostachys zeylanica* L. Hook.	Non-forest
Ophioglossaceae	*Ophioglossum reticulatum* L.	Non-forest
Polypodiaceae	*Microsorum scolopendria* (Burm. f.) Copel.	Non-forest
Pteridaceae	*Adiantum latifolium* Lam.	Non-forest
Pteridaceae	*Pityrogramma calomelanos* (L.) Link	Non-forest

Table 3.1 continued

Family	Species name	Group
Pteridaceae	*Taenitis blechnoides* (Willd.) Sw.	Forest
Schizaeaceae	*Lygodium circinnatum* (Burm. f.) Sw.	Forest
Schizaeaceae	*Lygodium flexuosum* (L.) Sw.	Non-forest
Schizaeaceae	*Lygodium longifolium* (Willd.) Sw.	Non-forest
Schizaeaceae	*Lygodium microphyllum* (Cav.) R.Br.	Non-forest
Schizaeaceae	*Lygodium salicifolium* Presl	Non-forest
Schizaeaceae	*Schizaea dichotoma* (L.) Sm.	Forest
Schizaeaceae	*Schizaea digitata* (L.) Sw.	Forest
Selaginellaceae	*Selaginella caulescens* (Wall.) Spring	Forest
Selaginellaceae	*Selaginella intermedia* (Bl.) Spring	Forest
Selaginellaceae	*Selaginella plana* (Desv.) Hieron.	Forest
Selaginellaceae	*Selaginella roxburghii* (Hk. & Gr.) Spring	Forest
Selaginellaceae	*Selaginella willdenowii* (Desv.) Baker	Non-forest
Thelypteridaceae	*Amphineuron* sp.	Non-forest
Thelypteridaceae	*Christella parasitica* (L.) Lév.	Non-forest
Thelypteridaceae	*Christella subpubescens* (Bl.) Holtt.	Non-forest
Thelypteridaceae	*Mesophlebion chlamydophorum* (C.Chr.) Holtt.	Forest
Thelypteridaceae	*Mesophlebion motleyanum* (Hook.) Holtt.	Forest
Thelypteridaceae	*Pronephrium glandulosum* (Bl.) Holtt.	Forest
Thelypteridaceae	*Pronephrium rubicundum* (v.A.v.R.) Holtt.	Forest
Thelypteridaceae	*Pronephrium* sp.	Forest
Thelypteridaceae	*Pronephrium triphyllum* (Sw.) Holtt.	Non-forest
Thelypteridaceae	*Sphaerostephanos heterocarpus* (Bl.) Holtt.	Forest

Families according to Kubitzki (1990).

At the plot level, differences between land use types for average number of (forest) species per plot were tested using one-way ANOVA and Tukey's HSD test.

At the landscape level, to analyse species–area relations the program EstimateS (Colwell, 1997) was used to randomise plot sequence 100,000 times for each land use type and derive average cumulative richness values.

A logarithmic equation of the form:

$$y = b \ln x + a \quad (1)$$

was fitted through the resulting points, where y is the cumulative number of species, b the scaling relation of species richness (beta diversity), x the cumulative number of 0.16 ha plots (area), and a a constant estimating the average richness for a single plot (alpha diversity).

The 'area' in the species–area curves represents a collection of non-adjacent 0.16 ha plots scattered over a vast landscape.

The distances between plots are comparable for forest and jungle rubber: the average distance between plots was for forest plots 42 km (S.E. = 3.6) and for jungle rubber plots 39 km (S.E. = 1.5). Non-parametric tests show that also the distributions of interplot distances are comparable for forest and jungle rubber. However, the interplot distances of the rubber plantation plots were different both in average (as high as 74 km, S.E. = 5.2) and in distribution. This is due to the fact that there are only two large rubber estates in the Jambi lowlands that have rubber trees of the higher age classes that we needed to include in the sampling, and those two estates are far apart (one near Muara Bungo, the other near Jambi town). As a result, long distances are over represented in the rubber plantation sample. This may have caused a slight overestimation of the slope parameters of the species–area curves for rubber plantations, but such overestimation would not seriously affect our main conclusions.

The slope parameters (*b*) found for the three land use types were compared statistically by linear regression over their common area range of 11 plots (1.76 ha).

3.5 Results

3.5.1 Plot level results

The average number of terrestrial pteridophyte species per plot in the current study was indeed higher in jungle rubber (on average 11.7 species) than in primary forest (on average 9.4 species), but not twice as high as found by Michon and De Foresta for herbs, and the difference found is not statistically significant.

Applying *a priori* ecological knowledge about our species, we find that the plot level species richness in jungle rubber and in rubber plantations is largely due to an increase in species that have their optima in environments other than the shady forest understorey, in

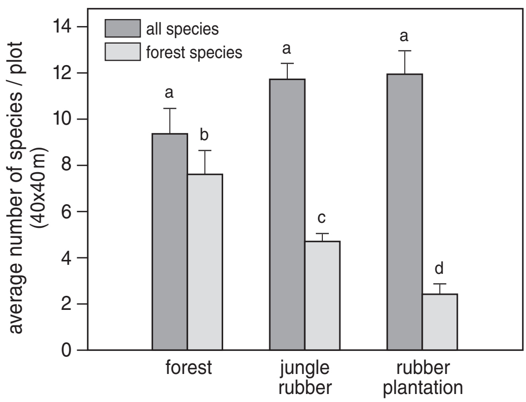

Figure 3.2 Number of terrestrial pteridophyte species per 0.16 ha plot. Means and their standard errors for three land use types: forest (n = 11), jungle rubber (n = 23) and rubber plantations (n = 17). Dark bars: all data; light bars: 'forest species' subset. Different letters indicate significant differences between land use types (Tukey's HSD test, P<0.05, see Table 3.2).

our classification 'non-forest species'. Figure 3.2 shows the differences in average number of species per plot for the three land use types. Differences are small and not statistically significant when all species are considered ($F[2,48] = 1.846$, $P = 0.169$), while those differences are large and statistically significant when only 'forest species' are considered ($F[2,48] = 18.112$, $P < 0.0005$; Table 3.2).

Table 3.2 Analysis of variance and post-hoc multiple comparisons for data in Figure 3.2: number of species per plot (all species, 'forest species').

	N	Mean of all species per plot	S.E. of the mean	Mean of 'forest species' per plot	S.E. of the mean
Forest	11	9.4	1.08	7.6	1.06
Jungle rubber	23	11.7	0.70	4.7	0.36
Rubber plantations	17	11.9	0.99	2.4	0.41
All land use types	51	11.2	0.52		

ANOVA

	Sum of squares	d.f.	Mean square	F	Significance
Number of terrestrial pteridophyte species					
Between groups	49.649	2	24.824	1.846	0.169
Within groups	645.528	48	13.448		
Total	695.176	50			
Number of 'forest species'					
Between groups	176.644	2	88.322	18.112	0.000
Within groups	234.062	48	4.876		
Total	410.706	50			

Multiple comparisons (Tukey's HSD). Dependent variable: number of 'forest species'

Land use (I)	Land use (J)	Mean difference (I – J)	S.E.	Significance	95% confidence interval	
					Lower bound	Upper bound
Primary forest	Jungle rubber	2.89*	0.81	0.002	0.94	4.85
	Rubber plantation	5.13*	0.85	0.000	3.07	7.20
Jungle rubber	Primary forest	–2.89*	0.81	0.002	–4.85	–0.94
	Rubber plantation	2.24*	0.71	0.007	0.53	3.95
Rubber plantation	Primary forest	–5.13*	0.85	0.000	–7.20	–3.07
	Jungle rubber	–2.24*	0.71	0.007	–3.95	–0.53

* The mean difference is significant at the 0.05 level.

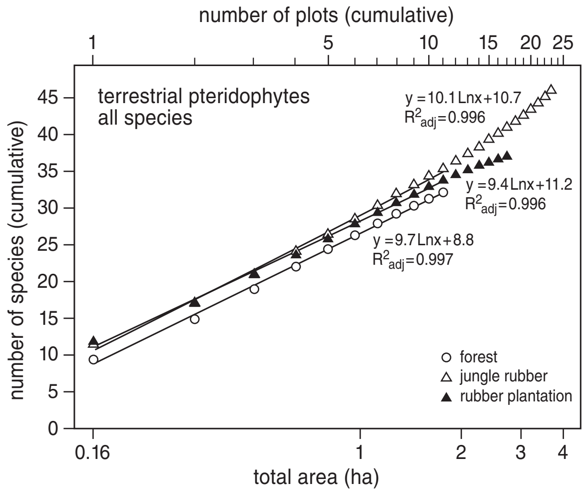

Figure 3.3 Species–area curves for terrestrial pteridophytes in forest, jungle rubber and rubber plantations. Plots were 0.16 ha each, non-adjacent and spread over a large area (see Figure 3.1). Plots were randomised 100,000 times to remove the effect of plot order.

3.5.2 Landscape level results, all species

Looking at the landscape level, we see that the species–area curves for pteridophytes in primary forest, jungle rubber and rubber plantations are close together (Figure 3.3).

We tested for equality of slopes of the regressions for the three land use types, and found that including interactions (which allows for different slopes) significantly improved the model ($F[2,27] = 4.005$, $P = 0.030$). The slope parameter of the jungle rubber land use type was significantly higher than the slope parameter of the rubber plantations land use type ($t = 2.827$, $P = 0.009$). The slope parameter of the forest was not significantly different from the slope parameters of the jungle rubber land use type and the rubber plantations land use type ($t = –1.534$, $P = 0.137$ and $t = 1.292$, $P = 0.207$, respectively). Figures 3.2 and 3.3 and the statistical testing make clear that the pattern at the plot scale is not reflected at the landscape scale. Jungle rubber shows higher beta diversity for terrestrial pteridophytes at the landscape scale than rubber plantations, despite similar plot level diversity.

3.5.3 Landscape level results, 'forest species'

After grouping species into 'forest species' and 'non-forest species' a second set of species–area curves was constructed based only on 'forest species'. These curves for 'forest species' (Figure 3.4) show the part of the total diversity in each land use type (as in Figure 3.3) that consists of species that prefer conditions prevalent in undisturbed forest. Slopes of the regression lines for 'forest species' (Table 3.3) differ significantly ($F[2,27] = 352.161$, $P < 0.0005$). The regression line for forest has a steeper slope than the regression lines for jungle rubber and rubber plantations ($t = 17.544$, $P < 0.0005$ and $t = 26.017$, $P < 0.0005$, respectively), and the regression line for jungle rubber has a steeper

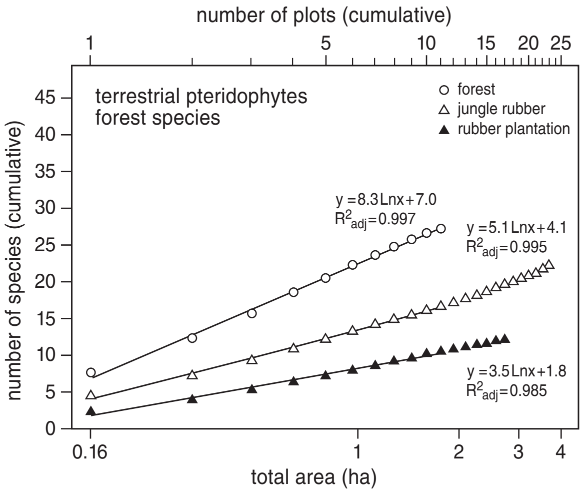

Figure 3.4 Species–area curves for 'forest species' subset of terrestrial pteridophytes in forest, jungle rubber and rubber plantations. Plots were 0.16 ha each, non-adjacent and spread over a large area (see Fig. 3.1). Plots were randomised 100,000 times to remove the effect of plot order.

slope than the regression line for rubber plantations ($t = 8.473$, $P < 0.0005$). The differences between the curves for primary forest (upper line), jungle rubber (middle line) and rubber plantations (lower line) show that the understorey environment of jungle rubber is much more forest-like than that of rubber plantations, but less than primary forest.

The number of jungle rubber plots added up to find the same number of 'forest species' in jungle rubber as in primary forest is progressively larger at the higher levels of species richness associated with larger areas. When S represents the number of 'forest species', we find at $S = 15$ we need 3.0 jungle rubber plots for each primary forest plot, at $S = 20$ we need 4.0 and at $S = 25$ we would need 5.3 jungle rubber plots for each primary forest plot.

In addition to the differences in diversity of 'forest species', our data show that some of the 'forest species' that are found in several primary forest plots never show up in jungle rubber plots, even though the sample contains twice as many jungle rubber plots

Table 3.3 Slopes and their standard errors for the species–area regressions (all species, 'forest species') in Figures 3.3 and 4.4.

	N	Slope parameter all species	S.E. of the slope	Slope parameter 'forest species'	S.E. of the slope
Forest	11	9.71	0.16	8.34	0.14
Jungle rubber	11	10.11	0.21	5.07	0.11
Rubber plantations	11	9.37	0.18	3.49	0.14

as primary forest plots. It is likely that the absence of those species, e.g. *Teratophyllum* spp. (Lomariopsidaceae) and *Trichomanes* spp. (Hymenophyllaceae), from the jungle rubber plots indicates that some primary forest species will never grow in jungle rubber.

3.6 Discussion and conclusions

3.6.1 Scale matters

The data clearly show that scaling relations differ between land use types and that plot level species richness does not directly indicate the (relative) richness of a land use type at the landscape scale. No single ratio can express the relative richness across different scales and conclusions as formulated by Leakey (1999) on the basis of the plot data of Michon and De Foresta (1995) cannot be trusted.

3.6.2 Conservation and production

Returning to the first question formulated in the introduction, we conclude that rubber production systems can indeed play some role in conservation of primary forest species (apparently providing forest-like habitat), but in places where primary forest is still present, priority should be given to conservation of remaining primary forest patches.

In places where primary forest is gone, jungle rubber can play a role in conservation of part of the primary forest species, while rubber plantations have little conservation value. In areas such as the Jambi lowlands where there is almost no primary forest left and where even logged-over forest is to a large extent already converted to plantations, jungle rubber might provide for intermediate levels of biodiversity while at the same time providing income to farmers (Van Noordwijk *et al.*, 1997). ICRAF is currently working in this area on a project to increase income of smallholders and promote biodiversity conservation by keeping production in old jungle rubber on a profitable level. Techniques of gap replanting and direct grafting in rubber agroforests using genetically improved rubber are developed to extend the lifespan of existing rubber agroforests, at the same time reducing the frequency of slash-and-burn in the landscape (Wibawa *et al.*, in review). With these techniques production could be raised while preserving the biodiversity associated with old jungle rubber.

3.6.3 Indicator groups

Species richness of terrestrial pteridophytes alone (without knowing the species or their ecological requirements) is not a useful indicator of habitat quality, as it discriminates poorly between the disturbed land use types and primary forest. *A priori* ecological information on the species involved is needed before terrestrial pteridophyte species can be used to indicate disturbance level or habitat quality of the forest understorey. If we would like to fully answer the question how much primary forest biodiversity is conserved in rubber agroforests we would have to sample most of the major taxonomic groups because different groups react in different ways to disturbance (see e.g. Thiollay, 1995, for birds). For each taxonomic group we would need enough samples to account for the variability in the data, and samples should cover a sufficiently large area to include different scales (plot level to landscape level). In addition, we need to know the ecological position (habitat requirements, guilds, etc.) of the species, as diversity alone does not give enough information for most taxonomic groups. Even so, such data collected within 'homogeneous' land use types cannot directly answer questions about the change in overall biodiversity value that can be expected if some types of land use will decrease, while others increase. The scaling rules within a land use type as given here will have to be (at least) complemented by assessments of species overlap between land use types. In addition assumptions have to be made about the maximum number of species present in each land use type as well as the minimum area required in each land use type to maintain healthy populations of those species.

It is understandable that available data are not compliant with all those requirements. Restricted by time and financial limits, researchers working in jungle rubber had to make choices with regard to the sampling dilemma, either researching all major groups but in small sample sizes and/or a small area, or getting ample information on one taxon and none on others. Difficult taxonomic groups in diverse tropical areas make the problem worse, as typically each sampling effort results in scores of new species to be named and described for the first time and existing ecological knowledge is limited. Pteridophytes proved in this study to be a relatively well-described group suitable to indicate local environmental conditions. Because the spores are wind dispersed their occurrence is not limited by presence of other organisms required for most seed dispersal or pollination. However, this characteristic of pteridophytes makes the group less suitable to represent biodiversity of other taxa. Hunting pressure and habitat fragmentation will affect some taxa more than others. Pteridophytes alone would probably provide us with a too optimistic view on biodiversity in jungle rubber.

As more results on different taxa become available it is no doubt possible to get a general idea of the order of magnitude of the contribution of jungle rubber to biodiversity conservation of tropical rain forest species. However, if the current trend of conversion to more intensively managed rubber or oil palm plantations continues we can be sure that hardly any biodiversity value will be left.

Acknowledgements

This research project was carried out in the framework of the Southeast Asian Regional Research Programme of the International Centre for Research in Agroforestry (ICRAF) in Bogor, Indonesia, as part of the 'Alternatives to Slash-and-Burn' Programme. It was sponsored by UNESCO (1995–1997) and the Netherlands Organisation for Scientific Research (NWO, 1997–2000). We thank Hubert de Foresta for providing valuable advice at the start of the project, and Dr. P.H. Hovenkamp and Dr. H.P. Nooteboom of the National Herbarium of the Netherlands for checking species identifications.

References

Alston, A.H.G. 1937. The Selaginellae of the Malay Islands. II. Sumatra. Bull. Jard. Bot. Buitenzorg Série III, 14 (2) (1937), pp. 175–186.

Backer, C.A., Posthumus, O. 1939. Varenflora voor Java. Overzicht der op Java voorkomende varens en varenachtigen, hare verspreiding, oekologie en toepassingen. 's Lands Plantentuin, Buitenzorg, Java.

Beukema, H., Stolle, F., van Noordwijk, M., De Foresta, H. 1997. Biodiversity in rubber agroforests. Paper presented at the Smallholder Rubber Agroforestry Project Workshop in Bogor, Indonesia. ICRAF Southeast Asian Regional Research Programme, Bogor.

Colwell, R.K. 1997. EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples, Version 5. User's Guide and application published at http://viceroy.eeb.uconn.edu/estimates.

Fletcher, W.W., Kirkwood, R.C. 1979. The Bracken Fern (*Pteridium aquilinum* L. (Kuhn)) its biology and control. In: Dyer, A.F. (Ed.), The Experimental Biology of Ferns. Academic Press, London, pp. 591–635.

Gouyon, A., De Foresta, H., Levang, P. 1993. Does 'jungle rubber' deserve its name? An analysis of rubber agroforestry systems in southeast Sumatra. Agrofor. Syst, 22 (1993), pp. 181–206.

Holttum, R.E. 1932. On *Stenochlaena, Lomariopsis* and *Teratophyllum* in the Malayan region. Gard. Bull. (Singapore), 5 (1932), pp. 245–313.

Holttum, R.E. 1938. The ecology of tropical pteridophytes. In: Verdoorn, F. (Ed.), Manual of Pteridology. Martinus Nijhoff, The Hague, pp. 420–450.

Holttum, R.E. 1959a. Gleicheniaceae. In: Van Steenis, C.G.G.J., Holttum, R.E. (Eds.), Flora Malesiana Ser. II Pteridophyta 1 (1). Martinus Nijhoff/Dr. W. Junk Publishers, The Hague, pp. 1–36.

Holttum, R.E. 1959b. Schizaeaceae. In: Van Steenis, C.G.G.J., Holttum, R.E. (Eds.), Flora Malesiana Ser. II Pteridophyta 1 (1). Martinus Nijhoff/Dr. W. Junk Publishers, The Hague, pp. 37–61.

Holttum, R.E. 1963. Cyatheaceae. In: Van Steenis, C.G.G.J., Holttum, R.E. (Eds.), Flora Malesiana Ser. II Pteridophyta 1 (2). Martinus Nijhoff/Dr. W. Junk Publishers, The Hague, pp. 65–176.

Holttum, R.E. 1966. Ferns of Malaya, 2nd ed. Botanic Gardens Singapore/Government Printing Office, Singapore.

Holttum, R.E. 1974. The fern-genus *Pleocnemia*. Kew Bull, 29 (2) (1974), pp. 341–357.

Holttum, R.E., Hennipman, E. 1978. Lomariopsis group. In: Van Steenis, C.G.G.J., Holttum, R.E. (Eds.), Flora Malesiana Ser. II Pteridophyta 1(4). Martinus Nijhoff/Dr. W. Junk Publishers, The Hague, pp. 255–330.

Holttum, R.E. 1981. Thelypteridaceae. In: Van Steenis, C.G.G.J., Holttum, R.E. (Eds.), Flora Malesiana Ser. II Pteridophyta 1(5). Martinus Nijhoff/Dr. W. Junk Publishers, The Hague, pp. 331–560.

Holttum, R.E. 1991. Tectaria group. In: Nooteboom, H.P. (Ed.), Flora Malesiana Ser. II Pteridophyta 2(1). Rijksherbarium/Hortus Botanicus, Leiden.

Kramer, K.U. 1971. Lindsaea group. In: Van Steenis, C.G.G.J., Holttum, R.E. (Eds.), Flora Malesiana Ser. II Pteridophyta 1(3). Martinus Nijhoff/Dr. W. Junk Publishers, The Hague, pp. 177–254.

Kubitzki, K. 1990. The Families and Genera of Vascular Plants. Springer-Verlag, Berlin.

Laumonier, Y. 1997. The vegetation and physiography of Sumatra. Geobotany, vol. 22. Kluwer Academic Publishers, Dordrecht.

Leakey, R.R.B. 1999. Agroforestry for biodiversity in farming systems. In: Collins, W.W., Qualset, C.O. (Eds.), Biodiversity in Agroecosystems. CRC Press, Boca Raton, USA, pp. 127–145.

Michon, G., De Foresta, H. 1995. The Indonesian agro-forest model. Forest resource management and biodiversity conservation. In: Halladay, P., Gilmour, D.A. (Eds.), Conserving Biodiversity Outside Protected Areas. The Role of Traditional Agro-ecosystems. IUCN Forest Conservation Programme, Andalucía, pp. 90–106.

Page, C.N. 1976. The taxonomy and phytogeography of bracken—a review. Bot. J. Linn. Soc, 73 (1976), pp. 1–34.

Pemberton, R.W., Ferriter, A.P. 1998. Old World Climbing Fern (*Lygodium microphyllum*), a dangerous invasive weed in Florida. Am. Fern J, 88 (4) (1998), pp. 165–175.

Piggot, A.G., Piggot, C.J. 1988. Ferns of Malaysia in Colour. Tropical Press Sdn. Bhd., Kuala Lumpur.

Rosenzweig, M.L. 1995. Species Diversity in Space and Time. Cambridge University Press, Cambridge.

Spicer, R.A., Burnham, R.J., Grant, P., Glicken, H. 1985. *Pityrogramma calomelanos*, the primary, post-eruption colonizer of Volcán Chichonal, Chiapas, Mexico. Am. Fern J, 75 (1) (1985), pp. 1–5.
Thiollay, J.-M. 1995. The role of traditional agroforests in the conservation of rain forest bird diversity in Sumatra. Conserv. Biol, 9 (2) (1995), pp. 335–353.
Tomich, T.P., van Noordwijk, M., Budidarsono, S., Gillison, A., Kusumanto, T., Murdiyarso, D., Stolle, F., Fagi, A.M. 1998. Alternatives to Slash-and-Burn in Indonesia. Summary report and synthesis of phase II. ASB-Indonesia Report no. 8. ICRAF S.E. Asia, Bogor, Indonesia.
Van Noordwijk, M., Tomich, T.P., Winahyu, R., Murdiyarso, D., Suyanto, Partoharjono, S., Fagi, A.M. 1995. Alternatives to Slash-and-Burn in Indonesia. Summary report of phase I. ASB-Indonesia Report no. 4. ICRAF S.E. Asia, Bogor, Indonesia.
Van Noordwijk, M., Tomich, T.P., De Foresta, H., Michon, G. 1997. To segregate—or to integrate? The question of balance between production and biodiversity conservation in complex agroforestry systems. Agrofor. Today, 9 (1) (1997), pp. 6–9.
Wibawa, G., Hendratno, S., van Noordwijk, M., in review. Cyclical or permanent smallholder rubber agroforestry systems with or without slash and burn. In: Proceedings of the ASA Symposium on Alternatives to Slash and Burn.
Wong, K.M. 1982. Critical observations on Peninsular Malaysian Selaginella. Gard. Bull. (Singapore), 35 (2) (1982), pp. 107–135.

Chapter 4

Terrestrial pteridophytes in rubber production systems: species composition, successional trends and the effects of land use practices

Hendrien Beukema

Abstract

Species composition of terrestrial pteridophytes was studied in the undergrowth of chronosequences of productive jungle rubber (*Hevea brasiliensis*) agroforests, aged 9 to 74 years old, and productive rubber plantations, aged 5 to 19 years old, in the lowlands of Jambi province, Sumatra. Species composition of terrestrial pteridophytes in primary forest served as a reference for the undisturbed situation. Jungle rubber agroforests consisted of a mixture of wild and planted vegetation dominated by rubber trees. These agroforests were usually only weeded for a few years after the rubber was planted, and developed a complex vegetation structure resembling a secondary forest. Rubber plantations were mostly monocultures, their vegetation structure and composition mainly determined by plantation management practices such as continued weeding and the use of herbicides. A total of 40 rubber plots and 11 primary forest plots measuring 40 m × 40 m (0.16 ha/plot) were sampled. Frequency of terrestrial pteridophyte species was assessed by counting species presence in 16 (10 m × 10 m) subplots in each plot, yielding a frequency score between 0 and 16 for each species in each plot. In addition, data was collected on the number of individuals of pteridophytes in the understorey, vegetation structure, litter layer, soil color, slope steepness and position of the plot on the hill slope. Interviews were held to collect information on age and management history of the rubber plots.

The 65 species of terrestrial pteridophytes in the dataset were classified in five groups according to apparent ecological similarity with respect to presence and abundance in plots of different land use types and ages, while a sixth group was formed containing those species that were only found in primary forest.

This grouping based on field data was compared to a previous species classification derived from literature that focused primarily on light requirements of species (see Chapter 3). The two classifications were generally in agreement. Groups found mostly in rubber plantations and (young) jungle rubber consisted predominantly of species that according to the literature preferred open or lightly shaded conditions. Species found mostly in jungle rubber appeared as an intermediate group, with half of the species preferring open or lightly shaded conditions and the other half preferring more shady conditions. The species that were found mostly in jungle rubber and primary forest all preferred shady conditions. The agreement between the grouping based on field data and the literature-based classification indicated that an *a priori* classification of terrestrial pteridophyte species into two groups based on light requirements may be used to interpret data in biodiversity and succession studies at the community level.

Change in species composition with plot age was more pronounced in jungle rubber than in rubber plantations. With increasing age of jungle rubber plots, species found mostly in rubber plantations and (young) jungle rubber, such as *Blechnum orientale*, *Microlepia speluncae*, *Nephrolepis biserrata, Stenochlaena palustris*, *Dicranopteris linearis* var. *linearis*, *Asplenium pellucidum*, *Lygodium microphyllum*, *Lygodium flexuosum*, *Christella subpubescens* and *Lygodium salicifolium*, became generally less abundant, especially after about 30 years, when some of these species disappeared altogether. In rubber plantations, some species found usually in jungle rubber and primary forest appeared in older plantations, but with lower abundance than in jungle rubber plots. Older rubber plantations were increasingly dominated by two ground-covering species, namely *Nephrolepis biserrata* and *Stenochlaena palustris*.

Frequencies of individual species were modeled with respect to plot age to detect successional patterns for a subset of 29 species that were common in the dataset. Patterns identified by modeling helped characterize individual species as either transient or climax species in secondary forest succession in the study area. Some recommendations are given with regard to the use of several species of terrestrial pteridophytes as indicator species for forest disturbance and forest regeneration.

4.1 Introduction

Jungle rubber agroforests in Sumatra consist of a mixture of wild and planted vegetation, dominated by planted rubber trees. Other trees, both wild and planted, as well as shrubs, vines and understorey vegetation growing together with the rubber make up an important part of the vegetation and structure of this Indonesian agroforestry system. From a biological point of view, jungle rubber can be seen as a type of secondary forest (Chokkalingam and De Jong 2001) where forest succession processes take place. Jungle rubber agroforests are established by slash-and-burn and the planting of rubber tree seedlings which is usually combined with a few years of rice cultivation and the growing of vegetables and herbs. Over time, there is an influx of wild species from surrounding areas. Pioneer species are replaced by species adapted to more shady conditions, and a multi-layered forest structure develops. However, since jungle rubber is an agroforestry system aimed at producing latex and other products, agricultural management practices also influence species composition, especially in young agroforests.

Rubber plantations on the other hand can not be seen as secondary forests. These intensive systems of rubber production, established by slash-and-burn and the planting of rubber clones or clonal seedlings, are mostly monocultures lacking in wild tree species. Rubber plantations typically consist of a single even-aged rubber tree layer, they usually lack a shrub layer, and the understorey vegetation is kept low while vines and aggressive weeds are controlled. The vegetation structure and composition is mainly determined by plantation management practices. Succession is limited to the understorey vegetation, where continued disturbance by weeding and the use of herbicides interferes with it.

In this chapter, I analyse terrestrial pteridophyte species composition along successional gradients (chronosequences) in jungle rubber and in rubber plantations, using the species composition of primary forest as a reference. Changes in species composition of understorey vegetation in both jungle rubber agroforests and rubber plantations are brought about mainly by succession processes, by disturbance associated with management practices, and by the interference of those two processes.

For terrestrial pteridophytes, which make up a large part of the understorey, shading is the most important environmental factor that changes with time while the vegetation grows taller. Shade affects the soil and air temperature, humidity of the air, and light conditions (Holttum 1966, p. 21). Torquebiau (1988) measured photosynthetically active radiation (PAR) in lowland forest in Pasir Mayang, one of the sampling areas. He found that daily total PAR at ground level, as a percentage of incident radiation above the forest, was less than one percent for mature forest, about 20 percent in a gap in the forest, and 3 percent in a transition zone between the gap and mature forest.

Shade increases with age in both jungle rubber agroforests and rubber plantations. Therefore, one can expect pteridophyte species preferring sunny conditions to be replaced over time by shade-tolerant species in both land use types. However, shading may be more important in jungle rubber than in rubber plantations due to a more complex vegetation structure (Gouyon *et al.* 1993) and a longer planting cycle. Variability in light conditions may also be greater in jungle rubber than in rubber plantations due to a more diversified forest structure. In addition, jungle rubber has a longer planting cycle. It gets much older than rubber plantations, allowing more time for succession to take place.

The effects of disturbance by management practices on species composition cannot be separated from the effects of succession processes in either system, but the level of disturbance and its likely impact is much higher in rubber plantations than in jungle rubber. Disturbance due to management practices is usually moderate in young jungle rubber agroforests, and very low in older agroforests, where it will hardly interfere with natural succession processes any longer. In rubber plantations, disturbance is high during most of the productive lifetime of the rubber trees. Therefore, in rubber plantations one can expect an increasing dominance of a few sturdy pteridophyte species that are able to withstand herbicide use and continued slashing.

The aims of this chapter are:

- To provide insight in the change in species composition of terrestrial pteridophytes during succession in a productive, post-fire secondary forest type in the lowland Dipterocarp forest area of Sumatra. Data on species composition in primary forest is provided as a reference.
- To group terrestrial pteridophyte species in the dataset with respect to disturbance and plot age, based on their presence and abundance in high-disturbance rubber plantations and low-disturbance jungle rubber of different age.
- To compare this grouping with a different, literature-based grouping (discussed in Chapter 3) that focused primarily on light requirements of species.
- To identify successional patterns and effects of management-related disturbance for individual terrestrial pteridophyte species that were common in the dataset. This was done by modeling their frequency values in high-disturbance rubber plantations and low-disturbance jungle rubber of different age, using HOF curves (Huisman *et al.* 1993).
- To explore which terrestrial pteridophyte species might be used as indicators of disturbance or of forest recovery in lowland Dipterocarp forest areas.

4.2 Method

4.2.1 Study area

The peneplain of Jambi province in Sumatra is a major rubber producing area with rather uniform soil and climate conditions (Whitten *et al.* 1987). The dissected peneplain consists of acid tuffaceous sediments and is composed of about 90% uplands with a flat to gently undulating landscape and mostly red-yellow podzolic soils and 10% river levees and floodplains with more fertile alluvial soils (Tomich *et al.* 1998). The sampling plots were all located in the uplands of the peneplain, in non-flooding areas at elevations ranging from 40 to 150 meters above sea level. For sampling locations see Figure 3.1 of Chapter 3.

Climate conditions are comparable throughout the lowlands of the Jambi peneplain. Temperatures vary little throughout the year. Average monthly maximum temperatures

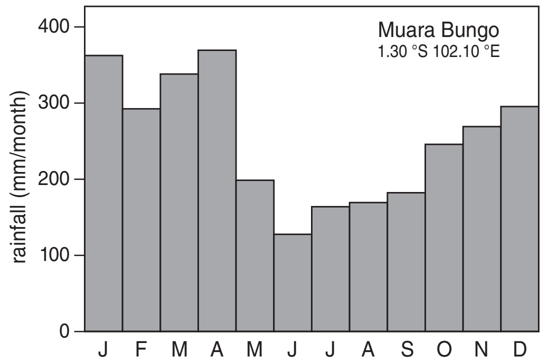

Figure 4.1 Rainfall distribution diagram of the Muara Bungo weather station. Data from 324 months between 1950 and 1976. (Source: www.worldclimate.com, derived from GHCN).

vary from 30.2 °C to 32.0 °C with a yearly average of 31.4 °C, while average monthly minimum temperatures vary from 22.1 °C to 22.9 °C with a yearly average of 22.5 °C (Jambi weather station, data from 190 months between 1960 and 1975. Source: www.worldclimate.com, derived from GHCN2Beta). On the agroclimatic map by Oldeman *et al.* (1979), the study area falls in the humid B1 climate category with 7 to 8 wet months (>200 mm rainfall / month) and 0 dry months (<100 mm rainfall / month) per year. Total rainfall is about 3000 mm per year, and rainfall distribution is of the equatorial type with the driest months from May to September (see Figure 4.1).

The sampling period (1996–1998) included the El Niño event of 1997, but the drought did not seriously affect terrestrial pteridophytes in the land use types sampled, at least not within the sampling period. Older fronds were occasionally found to be discoloured or wilted, but younger fronds of the same plant were usually not affected, and no plants were found to have died from lack of rain. Soil moisture and dew probably provided enough water.

4.2.2 Management history data

Sampling plots were located in jungle rubber agroforests (23 plots), rubber plantations (17 plots) and patches of primary mixed Dipterocarp rain forest (11 plots) in the Jambi peneplain. The sampled rubber plots were all productive and regularly tapped. Rubber plots were selected by age to form a chronosequence for each rubber land use type. Interviews were held with owners or managers of all 40 rubber plots to collect information on age and management history. For one of the jungle rubber plots, only the age could be ascertained but no detailed management information could be obtained. For company-owned plantations, interviews were held with plantation staff.

4.2.3 Soil and terrain data

Digital elevation data (F. Stolle, unpublished data) and a soil map (Muara Bungo Sheet 0914 Sumatra, see Wahyunto *et al.* 1990) were used to choose plot locations in such a way that altitude and soil type would be as similar as possible for the three land use types. Soil color of wet topsoil (0–5 cm) was recorded using Munsell soil color charts (Munsell color 1994 rev. ed.) in all but one of the plots. One recording was discarded because the soil had a mixture of colors (mottling) while no mottling was found in any other recording. Slope steepness was recorded for all plots using a Suunto clinometer. For plots on sloping land, the position of the plot was noted with regard to four zones on the hill slope: top, shoulder, midslope, or foot (or a combination of zones). Plots were not selected for their specific slope steepness or position on the slope.

4.2.4 Vegetation structure data

Percentage cover was estimated for the litter layer, and for four vegetation layers defined by height of the vegetation: < 1 m, 1–4 m, 4–20 m, and > 20 m high. Maximum tree height in each plot was measured using a Suunto clinometer. The thickness of the litter layer was measured with a ruler both in its natural condition and after pressing down the litter to compact it. Plots measured 40 m × 40 m and were divided into 16 subplots of 10 m × 10 m. Cover estimates and litter measurements were collected at the center of each of the 16 subplots, and averaged per plot.

The number of individuals per plot of pteridophytes in the understorey, regardless of species, was estimated by point-centered quarter method (see Mueller-Dombois and Ellenberg 1974), taking 4 distance measurements from each intersection point of the 16 subplots (25 times 4 measurements per plot), in 31 plots. The other 20 plots, including all of the primary forest plots, held too few individuals for this method, so individuals were counted instead. The point-centered quarter method is based on the assumption of randomly distributed individuals. However, some clumping occurs naturally in pteridophytes, while in rubber plantations the understorey vegetation is sometimes restricted to the interrows, which may produce an effect similar to clumping. The effects of non-random distribution may have been balanced by the mixture of species and the large number of measurements (100 per plot). There were 5 species for which 'individuals' could not be easily discerned, either because the species had long-creeping rhizomes (*Pteridium caudatum*, *Dicranopteris linearis*, *Pronephrium triphyllum*), were scrambling (*Stenochlaena palustris*) or had spreading runners (*Nephrolepis biserrata*). For these species, the aboveground 'units' were counted as if they were individuals.

Cover percentage of terrestrial pteridophytes in the whole plot was estimated for 34 of the 51 plots. In all primary forest plots, cover percentage was around 1%. Since differences smaller than one percent are hard to estimate in large plots, estimated cover was only recorded in two primary forest plots, and a standard error for this land use type was not calculated.

4.2.5 Pteridophyte data

Terrestrial pteridophytes were defined as all pteridophytes rooted in the soil substrate, and included climbing species. Standard plots of 40 m × 40 m (0.16 ha/plot) were established in jungle rubber (23 plots), rubber plantations (17 plots) and primary forest (11 plots). Plots were subdivided into 16 subplots of 10 m × 10 m each. Counting presence of terrestrial pteridophyte species in the 16 subplots of each plot resulted in a frequency score between 0 and 16 for each species in each plot. The frequency scores served as a measure of the importance of species in plots. For almost all of the species, frequency scores reflected abundance patterns of species as observed in the field.

Plots were located away from forest edges and roadsides to avoid edge effects, however small paths used by rubber tappers were not avoided. Plots were located well away from rivers and streams to avoid rheophytes.

Two varieties of *Dicranopteris linearis*, namely *D. linearis* var. *linearis* and *D. linearis* var. *subpectinata*, were treated as two separate species. This was done because I noticed in the field that they apparently have different ecological preferences, and are easily distinguished by their different branching patterns (see Holttum 1966, p. 630). *Trichomanes javanicum* Bl. and *Trichomanes singaporeanum* (v.d.B.) v.A.v.R. on the other hand are two different species but were analysed as one species. This was done because infertile individuals of the two species could not be distinguished. However, I could distinguish both of them from the only other *Trichomanes* species collected, which was *Trichomanes obscurum* Bl..

4.2.6 Data analysis

Data analysis consisted of two components: the ecological grouping of all 65 species in the dataset in a classification table, and the modeling of abundance patterns of individual species with respect to plot age, which was done for a subset of 29 species. Chronosequences were analysed separately for jungle rubber and rubber plantations because of the differences between the land use types regarding the level and duration of disturbance by management practices. However, there were a few species for which similar frequency values were found in rubber plantation plots and jungle rubber plots of similar age, and for those species the data from both land use types was analysed together in the individual species modeling.

For the species classification, I first selected a subset of species that were common in the dataset to form the basis of ecological species groups. Those species were placed in five groups according to apparent similarity with respect to presence and abundance in plots of different land use types and age. A classification table (matrix), presenting frequency data of all species, was made to provide insight in the differences in species composition among land use types as well as in the change in species composition with age of the two rubber land use types. The plots (columns) were arranged first by land use type (rubber plantation plots, jungle rubber plots, primary forest plots) and secondly by age of the rubber plots. Species (rows) were arranged by ecological group. First the subset of species on which the five groups were based was placed in the classification table. A sixth group was formed containing those species that were only found in primary forest. Then all other species in the dataset were assigned to a group based on their frequency values, and were accordingly positioned in the classification table.

Whereas the classification was based predominantly on the occurrence and abundance of species in three land use types including primary forest, the modeling of individual species allowed for analysis of successional trends in the rubber land use types. The

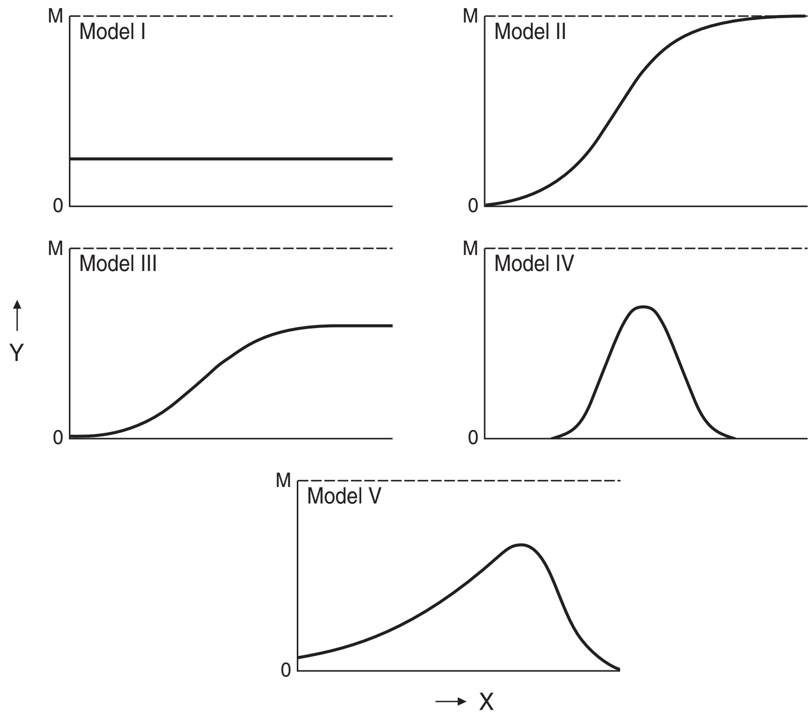

Figure 4.2 HOF models. Hierarchical set of five descriptive models for species response analysis as proposed by Huisman *et al.* (1993). Models are ranked by increasing complexity. Model I: no trend. Model II: increasing or decreasing trend. Model III: increasing or decreasing trend bounded below the maximum attainable response M. Model IV: symmetrical response curve. Model V: skewed response curve (can be skewed left or right).

individual species modeling involved analysis of frequency data of 29 species in rubber plots of different age, with the aim of detecting successional patterns. Patterns identified by modeling helped characterize individual species and groups of species as either transient or climax species in secondary forest succession in the study area. For species that were abundant in both rubber plantations and jungle rubber, modeling also helped to clarify differences or similarities in their response to the difference in management-related disturbance in rubber plantation plots and jungle rubber plots of similar age. Finally, results of modeling facilitated the selection of species with clear abundance patterns in relation to disturbance and forest age that could serve as indicators of forest disturbance and/or forest regeneration.

Occurrence of a species in at least 4 rubber plantation plots or 4 jungle rubber plots was regarded as a minimum requirement for modeling. Based on this requirement, 29 species were selected that were sufficiently common in the dataset for modeling.

To base models on as many data points as possible, I investigated whether for some of those 29 species the data points from rubber plantation plots and jungle rubber plots could be lumped together to produce a single model for both land use types. I took a subset of rubber plantation plots and jungle rubber plots within the age range of 9 to 21 years, which is the age range in the dataset that the two land use types have in common. I then selected the species that occurred in at least 3 rubber plantation plots and 3 jungle rubber plots within this age range. For each of those species, I compared the means and variances of their frequencies in rubber plantation plots (N = 12, aged 9–19 years) and jungle rubber plots (N = 9, aged 9–21 years) in the subset of plots of similar age. Scatterplots were visually inspected to check and confirm similarity of abundance patterns. Species that showed no statistically significant differences were modeled based on all rubber plots together (N = 40).

The hierarchical set of five models (see Figure 4.2) proposed by Huisman *et al.* (1993) was used to model abundance patterns of the 29 species with regard to the chronosequence of plots of different age, using frequencies (Y-axis) from 1 to 16, the number of subplots occupied per plot.

A syntax file in SPSS version 11.5 was used to run the models. Parameters of the models were estimated by non-linear regression, whereby the residual sum of squares was minimized by iteration. All five models were run for each selected species, after which the F statistic was used to compare R^2 values of the models and select the best model for the species, as recommended by Huisman *et al.* (1993). After selecting the best model for each of the modeled species, curves were drawn with their scatterplots, using the appropriate parameter values. If modeled species were present in primary forest plots, frequencies in the 11 primary forest plots were averaged and added to the figure as a reference point.

4.3 Plot characteristics

4.3.1 Management history of primary forest plots

The primary forest was old growth forest without visible traces of timber cutting and without known history of logging or shifting cultivation, the only human use being limited collection of non-timber forest products and hunting.

4.3.2 Management history of jungle rubber plots

All 23 jungle rubber plots were privately owned by farmers and were not part of a project. The age of sampled jungle rubber plots varied from 9 to 74 years, while the age of sampled rubber plantations was 5 to 19 years old. These age ranges represent the productive lifespan of jungle rubber and rubber plantations typically found in Jambi.

For the establishment of most of the jungle rubber agroforests, all previous vegetation was cleared by slash-and-burn, while in only 3 plots some large trees survived. Those were left standing because the farmer had to cut down primary forest without the use of a chainsaw. Rice and vegetables were planted after slash-and-burn in 73% of jungle rubber plots, while in the remaining plots only vegetables were planted alongside the rubber. On average, rice and/or vegetables were cultivated for 2 years. Weed control in jungle rubber plots consisted of slashing with a machete, usually only for the first two or three years

Figure 4.3 History of weed control. The number of consecutive years of weed control applied following slash-and-burn is displayed for jungle rubber and rubber plantation plots of different age. Filled dots: weeding in jungle rubber. Open dots: weeding in rubber plantations. Filled triangles: herbicides in rubber plantations. Plots on the x = y line had been weeded and/or treated with herbicides each year up to the year of sampling. Weeding consisted of slashing with a machete in both land use types, sometimes supplemented by hoeing in rubber plantations (see text).

after slash-and-burn (see Figure 4.3), while farmers lived in temporary housing on the new field. No herbicides, pesticides or fertilizers were used in jungle rubber plots.

Rubber seedlings for planting in jungle rubber plots were grown from seed collected in other (productive) jungle rubber agroforests. Rubber planting density in jungle rubber plots ranged from 450 to 3400 seedlings (sometimes seeds) per hectare with an average of 1000 per ha. Rubber seedling mortality as estimated by farmers averaged 425 per ha. Replacement seedlings were planted in 60% of jungle rubber plots, with an average of 160 replacements per ha. Other useful trees and perennials were planted with the rubber in all but two of the jungle rubber plots, on average 6 species with an average planting density of 50 trees per ha.

A wooden fence was erected around two of the jungle rubber plots to protect against vertebrate pests, while in three other plots poison was used for that purpose. After two to three years, farmers usually left the temporary housing and allowed the vegetation to grow tall. Most farmers kept checking on their unproductive jungle rubber plots more or less regularly, on average about once a month, for minor adjustments.

Some timber trees were allowed to grow spontaneously, as well as an average of 4 species of other desired trees and perennials in most of the jungle rubber plots. Those occurred with a density of 29 trees (or clumps, e.g. bamboo) per hectare. Undesired trees were removed by ring-barking in 63% of jungle rubber plots, usually only once, when the plot was first opened for tapping. Maintenance in productive rubber was usually limited to keeping paths to rubber trees open. From 39% of the jungle rubber plots, some trees were harvested for timber, while non-timber forest products were harvested from all jungle rubber plots.

Farm animals (mostly water buffalo, some cattle and goats) were kept away from most jungle rubber but were allowed to pass occasionally through six of the plots and to browse in another three plots.

4.3.3 Management history of rubber plantation plots

Five of the rubber plantations were privately owned by farmers and were not part of a project. The other 12 rubber plantations were part of two types of government projects: NES/PIR projects (10 plantations) and P2WK projects (2 plantations). Of those 12 project-related plantations, 7 were privately owned while 5 were owned by the state company PTP Nusantara VI. Management of project-related plantations was partly or completely regulated by the project administration.

Rubber plantations were all established after complete slash-and-burn of the previous vegetation except for one occasion where a farmer spared a valuable durian fruit tree (*Durio zibethinus* Murr.) from the old rubber agroforest that he was replanting.

In the 10 plantations belonging to NES/PIR projects, no rice or vegetables were grown, and a legume cover crop was sown. Rice and vegetables were planted after slash-and-burn in 71% of the remaining rubber plantations, while in 29% only vegetables were planted alongside the rubber. On average, rice and/or vegetables were cultivated for 2 years in those plantations. In two plantations, a legume cover crop was sown after one year of rice and/or vegetable cultivation.

Weed control in rubber plantations consisted of slashing with a machete, at least once a year, for almost the entire lifespan of the plantation, in combination with the use of herbicides in all but one of the plantations for variable lengths of time (see Figure 4.3). Herbicides contained glyphosate (roundup, polaris), paraquat (paracol, gramoxone) or metsulfuron methyl (ally). Each year, at least one of the several types of herbicide was usually applied, while frequency of application of each specific type of herbicide depended on the age of the rubber, the (perceived) need for application, the availability of the particular herbicide, and the financial means of private owners. In 53% of the plantations, a hoe was used for manual weeding in addition to a machete, usually for shorter time periods and especially during the first few years in privately owned plantations.

Pesticides were used in 75% of rubber plantations, and fertilizers were applied around rubber trees in all but one of the rubber plantations. Fertilizers were applied every year in five estate plantations in the PIR/NES estates and in two privately owned plantations, and for an average of 7 consecutive years after planting in the other nine plantations.

Planting material for rubber plantations consisted of either clones or clonal seedlings. Clones were mostly GT1. Clonal seedlings were seedlings grown from seed collected in (productive) rubber plantations that were planted with clones. Rubber planting density in plantations ranged from 375 to 600 clones or clonal seedlings per hectare, with an average of 509 per ha. Rubber clone or clonal seedling mortality as estimated by farmers averaged 127 per ha. Replacement clones or clonal seedlings were planted in 57% of plantations, with an average of 105 replacements per ha. In the 10 plantations belonging to NES/PIR projects, no other tree species were planted. In the other 7 plantations, useful trees were planted with the rubber: in 6 plantations with an average planting density of 26 trees per ha, and in one plantation with a planting density of 446 per ha.

Plantations belonging to NES/PIR projects were not fenced, while around 57% of the other plantations a wooden fence was erected to protect against vertebrate pests. Poison was used against vertebrate pests in 71% of all sampled rubber plantations. Most farmers lived in temporary or permanent housing on or near the plantation, and checked the plantation daily during the unproductive period.

In 5 of the privately owned plantations, an average of 2 species of desired trees and perennials, such as fruit trees, coffee and bamboo, was allowed to grow spontaneously. These occurred with an average density of 5 trees (or clumps) per hectare in 4 of those plantations. Plantations supplied no timber and a limited number of non-timber forest products.

Farm animals (mostly goats, some cattle and water buffalo) were kept away from most rubber plantations but were allowed to pass occasionally through 2 of the plantations and to browse in another 5 plantations.

4.3.4 Soil and terrain

Soils on the peneplain are poor oxi- and ultisols (Van Noordwijk *et al.* 1998). According to the soil map (Wahyunto *et al.* 1990), dominant soils at the plot locations belonged to the Hapludox, Dystropepts and Kandiudults groups. Soils were very deep, well drained, excessively to strongly acid (pH 3.5 to 5.5, Wahyunto *et al.* 1990), and had a low soil fertility status (Wahyunto *et al.* 1990, Van Noordwijk *et al.* 1998). Soil color varied relatively little between plots and between land use types. A summary of soil color recordings is presented in Table 4.1.

Munsell value and chroma scores of rubber plots were lower than those of primary forest plots, reflecting a history of slash-and-burn land clearing that has darkened the soil (Ketterings and Bigham 2000). Soils under rubber plantations were generally slightly more red, mostly 7.5YR, than soils under primary forest and jungle rubber, which had hues mostly of 10YR. Reddening of soils is also fire-related in this area (Ketterings and Bigham 2000).

I was able to collect information on past land use for 11 rubber plantations and 18 jungle rubber agroforests in the sample. For more than half of those rubber plots, namely

Table 4.1 Percentage of plots in each land use type by Munsell hue, value and chroma scores of their soil.

Munsell			**Primary forest** N = 10	**Jungle rubber** N = 23	**Rubber plantations** N = 16
Hue	7.5YR	more red	30	22	62
	10YR	more yellow	70	78	38
Value	4	darker	10	57	75
	5	|	60	43	25
	6	lighter	30	0	0
Chroma	3	less color	0	13	6
	4	|	20	30	31
	6	more color	80	57	63

55% of the rubber plantations and 61% of the jungle rubber agroforests, past vegetation consisted of primary forest or (partly) logged forest, and land had been burned by farmers only once to establish the current rubber land use. The rest of those 29 rubber plots were established on land that had been burned at least twice for cultivation. Past land use for those plots consisted of old jungle rubber (27%), old secondary forest (9%), or (secondary) forest with *Imperata cylindrica* grass (9%) for plots currently under rubber plantations; and old secondary forest (22%), young secondary forest (11%), or old jungle rubber (6%) for plots currently under jungle rubber.

A summary of slope steepness recordings is presented in Table 4.2. The fragments of primary forest that were still present in the area were situated mostly on undulating to rolling land, whereas jungle rubber was mostly found on flat to undulating land and rubber plantations were mostly found on flat land.

A summary of recordings of plot position with regard to four zones on the hill slope is presented in Table 4.3. Primary forest plots were mostly located on the shoulder or midslope of hills, whereas jungle rubber and rubber plantation plots that were on sloping land were most often located on hilltops.

Table 4.2 Slope steepness of plots in primary forest, jungle rubber and rubber plantations. Values represent the percentage of plots in each land use type where slope steepness within a slope class was recorded. Steepness classes and descriptions follow Wahyunto *et al.* 1990.

Slope steepness class	Description	Primary forest (% of plots)	Jungle rubber (% of plots)	Rubber plantations (% of plots)
0 – 2%	flat	9.1	60.9	82.4
3 – 7%	undulating	18.2	21.7	11.8
8 – 15%	rolling	63.6	13.0	5.9
16 – 20%	moderately steep	9.1	4.3	0
N (plots)		N = 11	N = 23	N = 17

Table 4.3 Position of primary forest, jungle rubber and rubber plantation plots. Values represent the percentage of plots in each land use type located in each plot position class.

Plot positioned on:	Primary forest (% of plots)	Jungle rubber (% of plots)	Rubber plantations (% of plots)
flat land	9.1	60.9	82.4
top of hill	16.7	20.3	11.8
shoulder of hill	39.4	9.4	5.9
midslope of hill	34.8	7.2	0
foot of hill	0	2.2	0
N (plots)	N = 11	N = 23	N = 17

4.3.5 Vegetation structure

Figure 4.4 shows percentage cover of four main vegetation layers by land use type, while Figure 4.5 shows average maximum tree height by land use type. Figure 4.6 shows litter cover and thickness of the litter layer. Jungle rubber plots are grouped by age: young jungle rubber of 9–26 years old (N = 10) and old jungle rubber of 32–74 years old (N = 13).

Rubber plantations consisted of a single tree layer, with low vegetation covering the ground underneath, and very little vegetation in between. Lianas were absent and the understorey vegetation consisted mainly of pteridophytes, grasses, sedges and *Melastoma malabathricum* L. (senduduk). Primary forest was the most layered vegetation (see also Laumonier 1997), with high emergent trees up to 60 m, lower trees, an intermediate layer of shrubs, small trees, palms, etc., and sparse ground cover. The vegetation structure of jungle rubber agroforests was intermediate between rubber plantations and primary forest, with old jungle rubber resembling primary forest more than young jungle rubber (see Figure 4.4).

However, trees were typically much larger in primary forest than in old jungle rubber (see Figure 4.5), which makes for an important difference between primary forest and jungle rubber. Primary forest had the sparsest ground cover (vegetation < 1 m) of all land

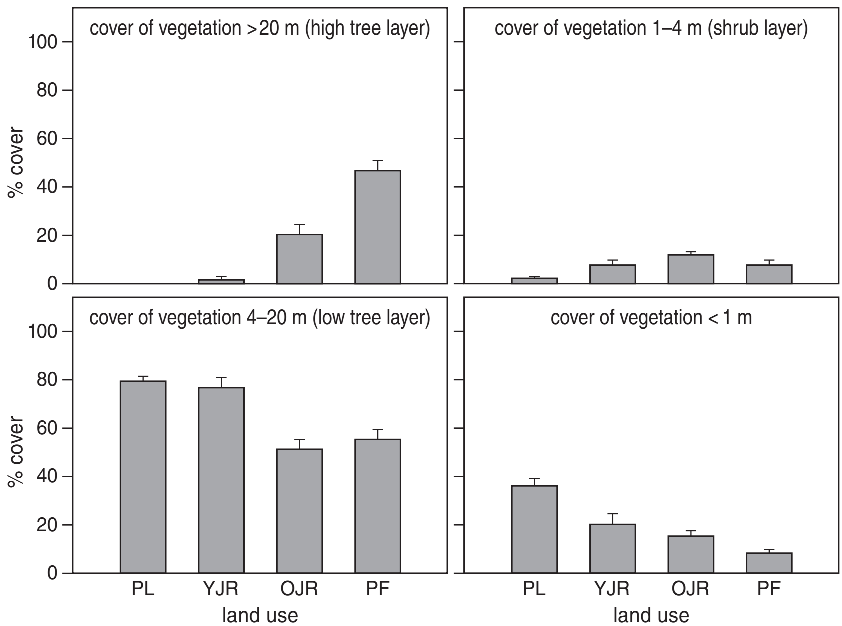

Figure 4.4 Vegetation structure of rubber plantations (PL, N = 17), young jungle rubber (YJR, N = 10), old jungle rubber (OJR, N = 13) and primary forest (PF, N = 11). Values are averaged estimated cover percentages of four main vegetation layers, defined by height of the vegetation: <1 m, 1 – 4 m, 4 – 20 m, and >20 m high. Means and their standard errors for each land use type were based on plot means, which were compiled from 16 estimates per layer in each plot.

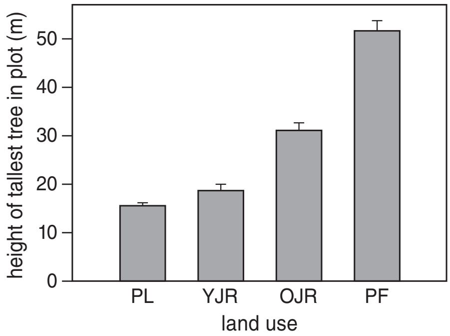

Figure 4.5 Tree height. Means and their standard errors of the height of the tallest tree in each of the rubber plantation plots (PL, N = 17), young jungle rubber plots (YJR, N = 10), old jungle rubber plots (OJR, N = 13) and primary forest plots (PF, N = 9).

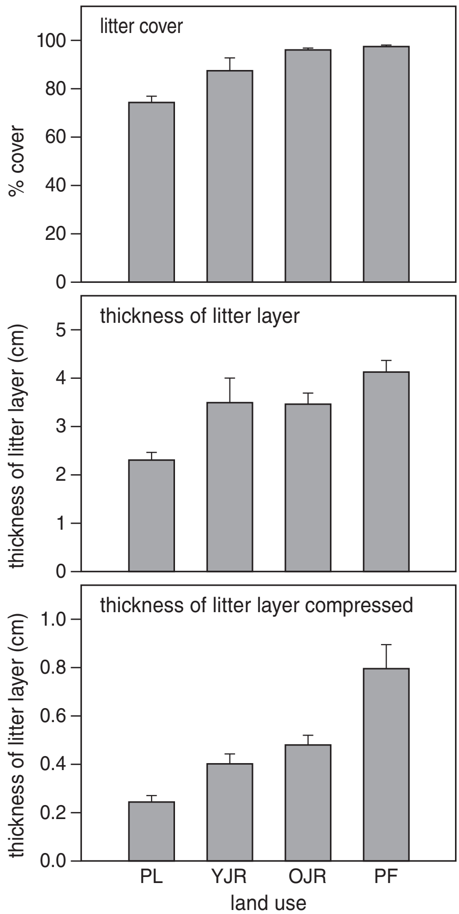

Figure 4.6 Litter cover percentage and thickness of the litter layer in rubber plantations (PL, N = 17), young jungle rubber (YJR, N = 10), old jungle rubber (OJR, N = 13) and primary forest (PF, N = 11). Means and their standard errors for each land use type were based on plot means, which were compiled from 16 estimates (for litter cover percentage) or measurements (for litter thickness) in each plot. The thickness of the litter layer was measured both in its natural condition and after pressing down the litter.

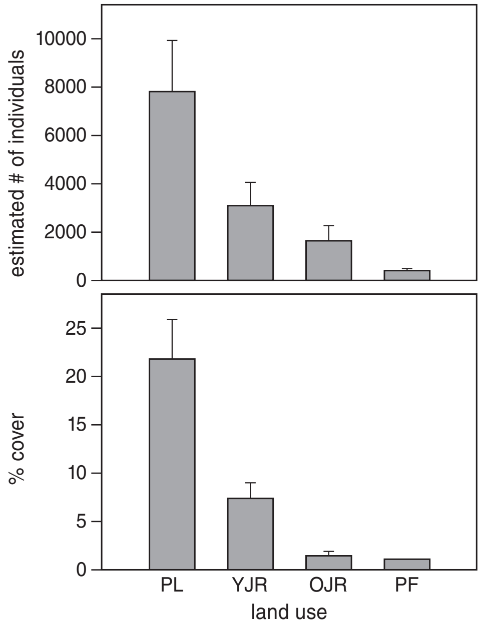

Figure 4.7 Abundance and cover of pteridophytes in the understorey, by land use type. Upper panel: means and their standard errors of the number of individuals per plot of pteridophytes in the understorey, either estimated by point-centered quarter method or counted, in rubber plantations (PL, estimated N = 14, counted N = 3), young jungle rubber (YJR, estimated N = 8, counted N = 2), old jungle rubber (OJR, estimated N = 9, counted N = 4) and primary forest (PF, counted N = 11). Lower panel: means and their standard errors of the estimated cover percentage of pteridophytes in the understorey of plots in rubber plantations (PL, N = 16), young jungle rubber (YJR, N = 6), old jungle rubber (OJR, N = 10) and primary forest (PF, N = 2).

use groups. Vegetation lower than 1 m was more varied in primary forest and jungle rubber than in rubber plantations, and consisted of pteridophytes, tree seedlings, rattan and other palms, pandanus, small-sized shrub species and other plants. Grasses, sedges and bamboo sometimes occurred in young jungle rubber.

Litter cover and thickness of the litter layer (see Figure 4.6) were lowest in rubber plantations and highest in primary forest, with values for jungle rubber in between. Thickness of the litter layer was relatively high in young jungle rubber due to the presence of curled-up leaves of *Macaranga* spp. in some of the plots; this effect disappeared when litter was compressed. Compressed litter in primary forest was relatively high because it contained more woody material (twigs, nuts) than the other land use types.

The estimated (or counted) number of individuals of pteridophytes in the understorey as well as the cover percentage of pteridophytes is summarized in Figure 4.7.

The number of individuals in rubber plantations was rather variable and increased with plantation age from about 500 per plot (0.16 ha) in the youngest plantations to about 15,000 per plot in the oldest plantations. The average number of individuals per plot and the variability were lower in young jungle rubber and lower again in old jungle rubber. In primary forest, where all individuals were counted, the average number of individuals was 415 per plot, which was the lowest average of the land use types.

Percentage cover of terrestrial pteridophytes followed a pattern similar to that of the number of individuals. Cover percentage was variable in rubber plantations and increased with plantation age from 1% cover in the youngest plantations to almost 50% in the oldest plantations, with an average cover percentage of 22%. Percentage cover of pteridophytes was higher in rubber plantations than in jungle rubber of similar age. In young jungle rubber, pteridophytes covered around 8%, in old jungle rubber around 2% and in primary forest pteridophyte cover was 1% or less.

4.4 Results

4.4.1 Classification of terrestrial pteridophytes

The classification table (Table 4.4) includes frequencies of all terrestrial pteridophyte species found in plots, as well as land use type and age of each plot, the group to which the species was assigned, and the classification of the species based on literature in Chapter 3. Groups' descriptions and the full species names of species in groups are listed below, in order of their appearance in the classification table. Species that were modeled are marked with an asterisk.

Group 1. Species found only or predominantly in rubber plantations.

Helminthostachys zeylanica L. Hook. *
Pteridium caudatum (L.) Maxon subsp. *yarrabense* (Domin) Parris *
Cyathea sp.2 *
Adiantum latifolium Lam. *
Asplenium longissimum Bl.
Pleocnemia irregularis (C. Presl) Holtt.
Microsorum scolopendria (Burm. f.) Copel.
Amphineuron spec.

Group 2. Species found more in rubber plantations than in jungle rubber, and rarely or not in primary forest.

Blechnum orientale L. *
Microlepia speluncae (L.) Moore *
Nephrolepis biserrata (Sw.) Schott *
Stenochlaena palustris (Burm.) Bedd. *
Pityrogramma calomelanos (L.) Link
Christella parasitica (L.) Lév.
Sphaerostephanos heterocarpus (Bl.) Holtt.
Asplenium glaucophyllum v.A.v.R.
Selaginella plana (Desv.) Hieron.
Cyathea sp.3

Group 3. Species found in rubber plantations and jungle rubber, and not in primary forest.

Dicranopteris linearis (Burm. f.) Underw. var. *linearis* *
Asplenium pellucidum Lam. *
Lygodium microphyllum (Cav.) R.Br. *
Lygodium flexuosum (L.) Sw. *
Christella subpubescens (Bl.) Holtt. *
Lygodium salicifolium Presl *
Pronephrium triphyllum (Sw.) Holtt. *

Group 4. Species found mostly in jungle rubber, less or not in rubber plantations and primary forest.

Selaginella willdenowii (Desv.) Baker *
Lygodium circinnatum (Burm. f.) Sw. *
Dicranopteris linearis (Burm. f.) Underw. var. *subpectinata* (Christ.) Holtt. *
Selaginella intermedia (Bl.) Spring *
Lygodium longifolium (Willd.) Sw. *
Schizaea dichotoma (L.) Sm. *
Lindsaea ensifolia Swartz *
Tectaria vasta (Bl.) Copel.
Lycopodium cernuum L.
Pronephrium spec.
Cyathea cf. *contaminans* (Hooker) Copel.
Diplazium pallidum Bl.
Ophioglossum reticulatum L.
Diplazium riparium Holtt.
Asplenium spec.

Group 5. Species found in jungle rubber and primary forest, and less or not in rubber plantations.

Taenitis blechnoides (Willd.) Sw. *
Blechnum finlaysonianum Hk. & Grev. *
Tectaria singaporeana (Wall. ex Hk. & Gr.) Copel. *
Lindsaea doryphora Kramer *
Mesophlebion chlamydophorum (C.Chr.) Holtt. *
Tectaria barberi (Hk.) Copel. *
Schizaea digitata (L.) Sw. *
Diplazium tomentosum Bl.
Tectaria fissa (Kunze) Holtt.
Diplazium malaccense C. Presl
Selaginella roxburghii (Hk. & Gr.) Spring
Selaginella caulescens (Wall.) Spring

Group 6. Species found only in primary forest.

Trichomanes javanicum Bl. / *T. singaporeanum* (Bosch) v.A.v.R.
Trichomanes obscurum Bl.
Lindsaea cultrata (Willd.) Swartz
Cyathea moluccana R. Br.
Diplazium crenatoserratum (Bl.) Moore
Pronephrium rubicundum (v.A.v.R.) Holtt.
Teratophyllum cf. *ludens* (Fée) Holtt.
Lindsaea cf. *repens* (Bory) Thw.
Lindsaea divergens Hk. & Grev.
Pronephrium glandulosum (Bl.) Holtt.
Teratophyllum cf. *rotundifoliatum* (R. Bonap.) Holtt.
Mesophlebion motleyanum (Hook.) Holtt.
Lindsaea parasitica (Roxb. ex Griffith) Hieron.

4.4.2 Comparison with literature-based classification

For each species, Table 4.4 shows in which of the six groups it was placed according to the classification based on frequency values, as well as in which class ('forest species' or 'non-forest species') it was placed in the *a priori* literature-based classification of Chapter 3. Species in groups 1, 2 and 3, found mostly in rubber plantations and (young) jungle rubber, were predominantly classified as 'non-forest species' in the literature-based classification. Species in group 4, found mostly in jungle rubber, appear as an intermediate group of species with half of the species classified as 'non-forest species' and the other half as 'forest species', while species in groups 5 and 6, found mostly in jungle rubber and primary forest, were all classified as 'forest species' in Chapter 3.

Throughout the dataset, 'non-forest species' were generally more abundant than 'forest species'. The 26 'non-forest species' occurred with an average frequency value of 4.6 in on average 13 plots, while the 36 species classified in chapter 3 as 'forest species' occurred with an average frequency value of 3.8 in on average 6 plots.

4.4.3 Modeled species

Frequencies of the 29 species that were most common in the dataset were modeled with respect to plot age to identify successional patterns and effects of management-related disturbance.

I first assessed for which species I could lump the frequency data of rubber plantation plots and jungle rubber plots. I found that 13 species were present in at least 3 plots in each land use type in the common age range of 9 to 21 years, and I compared each of those species for equality of the means and variances of their frequencies in rubber plantation plots and jungle rubber plots within this common age range. I found significant differences for 6 species while for 7 species no significant differences were found. Based on the results for those 7 species (Table 4.5), and visual inspection of their scatterplots, I decided to lump the data for rubber plantation plots and jungle rubber plots for modeling each of those 7 species.

Table 4.4 Classification of terrestrial pteridophytes. Frequencies of terrestrial pteridophytes in rubber plantation plots (N = 17, aged 5–19 years), jungle rubber plots (N = 23, aged 9–74 years) and primary forest plots (N = 11). Frequency values of 0 to 16 represent presence/absence in 16 subplots of 10 m × 10 m of each plot of 40 m × 40 m. Plots were arranged first by land use type and secondly by age of the rubber plots. Groups' descriptions and full species names are listed in the text. Species marked with an asterisk were also modeled. Class refers to an earlier classification based on literature (see chapter 3): F = 'forest species', NF = 'non-forest species', NC = not classified.

			Rubber plantations																	Jungle rubber																							Primary forest										
		plot number	52	50	51	32	41	53	54	46	48	42	43	35	44	47	49	39	40	34	36	33	45	8	28	29	38	37	31	7	27	22	30	19	20	3	17	10	4	9	18	5	6	11	12	13	14	15	21	23	24	25	26
class	group	plot age (yrs)	5	7	7	8	8	9	9	12	12	13	14	16	16	16	16	17	19	9	9	12	13	14	14	14	16	21	26	32	32	33	33	38	38	39	52	53	54	55	57	74											
NF	1	helmizey*	9	3	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
NF	1	ptericau*	.	.	.	.	1	14	.	.	3	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
NC	1	cyathsp2*	.	.	.	.	.	.	.	.	.	4	7	.	1	.	.	3	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
NF	1	adianlat*	1	.	.	.	.	.	5	5	.	2	5	.	.	.	2	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
NF	1	asplelon	.	.	3	.	.	.	.	.	.	4	.	.	.	.	.	.	7	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
F	1	pleocirr	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
NF	1	microsco	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
NF	1	amphispc	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
NF	2	blechori*	1	2	.	.	.	1	3	5	2	.	12	1	12	1	.	8	.	.	1	.	.	1	.	.	.	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
NF	2	microspe*	10	.	.	.	2	.	.	12	2	12	16	.	13	2	.	9	15	.	1	4	.	4	.	.	3	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
NF	2	nephrbis*	11	5	15	14	8	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	16	15	11	15	11	14	2	2	1	4	6	.	1	.	1	5	6	3	3	2	1	.	.	.	.	1	.	.	.	.	.
NF	2	stenopal*	1	.	8	11	12	16	1	8	12	14	16	16	16	9	15	16	16	15	10	16	2	14	.	14	4	1	14	2	12	5	1	2	7	2	10	8	8	2	13	.	.	.	.	.	.	.	.	.	.	1	.
NF	2	pityrcal	3	.	.	.	.	.	.	.	.	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
NF	2	chrispar	3	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
F	2	sphaehet	.	.	.	.	.	.	1	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
NF	2	asplegla	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
F	2	selagpla	.	.	6	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
NC	2	cyathsp3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.
NF	3	dicralil*	.	4	.	3	10	5	.	12	10	.	7	7	6	14	1	3	.	1	9	6	.	.	.	.	.	11	10	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
F	3	asplepel*	.	.	.	.	.	.	3	.	.	.	.	.	2	7	11	.	.	1	.	.	8	4	1	10	.	4	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
NF	3	lygodmic*	2	12	.	5	1	3	4	9	6	4	14	1	13	.	4	5	.	3	12	7	.	1	.	.	.	14	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
NF	3	lygodfle*	15	12	.	2	.	8	16	3	2	.	2	1	5	.	.	.	.	.	11	.	.	.	.	.	3	5	2	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
NF	3	chrissub*	9	.	.	.	.	.	7	.	.	.	.	.	.	.	1	.	.	.	.	4	1	.	2	8	.	2	.	.	.	.	15	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
NF	3	lygodsal*	16	14	.	1	3	1	.	7	6	3	10	.	15	.	4	1	.	4	12	3	.	2	5	16	5	16	2	.	3	1	9	.	4	.	3	2	3	.	1	.	.	.	.	.	.	.	.	.	.	.	.
NF	3	pronetri*	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	1	.	.	.	.	.	.	.	.	.	2	.	.	1	.	1	.	.	.	1	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.

			Rubber plantations																	Jungle rubber																							Primary forest										
		plot number	52	50	51	32	41	53	54	46	48	42	43	35	44	47	49	39	40	34	36	33	45	8	28	29	38	37	31	7	27	22	30	19	20	3	17	10	4	9	18	5	6	11	12	13	14	15	21	23	24	25	26
class	group	plot age (yrs)	5	7	7	8	8	9	9	12	12	13	14	16	16	16	16	17	19	9	9	12	13	14	14	14	16	21	26	32	32	33	33	38	38	39	52	53	54	55	57	74											
NF	4	selagwil*	.	.	9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	16	.	16	11	.	.	.	.	16	.	10	2	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
F	4	lygodcir*	1	3	9	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	15	.	16	7	.	.	.	.	14	.	16	1	.	.	.	.	.	.	.	.	.	.	.	15	.	.	.	.	.	.	.
NF	4	dicralis*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	1	.	2	.	.	.	6	.	.	.	.	8	.	.	4	.	.	16	8	4	1	.	4	.	5	.	3	.	.	.	1	.	.	.	1	.
F	4	selagint*	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	1	2	.	11	.	.	2	.	1	16	12	12	.	16	.	.	.	.	.	13	.	.	.	.	1
NF	4	lygodlon*	1	12	.	1	.	.	.	.	2	.	.	.	.	.	.	.	.	.	11	2	6	.	4	.	1	1	.	.	3	7	8	5	14	13	13	3	4	.	13	15	.	.	.	1	4	.	.	2	.	1	.
F	4	schizdic*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	4	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.
NF	4	lindsens*	1	13	.	.	3	2	.	14	16	2	15	6	11	11	14	11	8	10	15	7	.	3	9	9	8	16	16	.	7	15	1	15	15	14	14	5	1	.	16	14	3	8	11	9	13	.	7	3	11	10	1
F	4	tectavas	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.
NF	4	lycopcer	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
F	4	pronespc	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
NF	4	cyathcfc	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
F	4	diplapal	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
NF	4	ophioret	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
F	4	diplarip	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.
NC	4	asplespc	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.
F	5	taenible*	.	.	.	1	.	3	1	13	16	.	12	10	10	6	13	8	10	5	14	15	6	15	16	15	16	16	16	8	13	16	1	12	16	16	16	16	16	16	16	16	6	4	16	16	15	16	15	16	16	14	13
F	5	blechfin*	.	.	.	.	.	.	.	1	.	1	1	.	2	.	1	8	1	.	3	6	.	3	.	.	2	2	7	1	.	2	.	.	2	.	.	9	.	.	.	2	1	5	3	.	6	3	1	.	3	7	.
F	5	tectasin*	.	.	.	.	.	.	.	.	.	.	.	2	1	.	.	1	.	3	2	8	.	16	.	.	2	3	.	15	.	.	.	.	.	.	.	1	.	16	.	.	.	.	.	.	.	14	1	8	.	.	.
F	5	lindsdor*	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	1	.	.	.	.	.	1	.	.	2	3	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	3	3	.	.
F	5	mesopchl*	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	9	.	.	2	.	5	1	.	.	.	.	1	.	.	1	.	5	.	.	.	.	3	.	.	.	1	3	2	.	.
F	5	tectabar*	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	1	.	.	.	1	.	.	.	.	.	.	5	.	1	.	.	.	1	2	.	11	1	.	2	11	.
F	5	schizdig*	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8	16	.	.	1	.	.	6	.	.	3	.	7	.	.	.	3	2	.	4	.	.	.	.	1	.	1	.	1
F	5	diplatom	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	7	.	.	.	.	.
F	5	tectafis	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	6	.	.	.	.	.
F	5	diplamal	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.
F	5	selagrox	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	1	13	.
F	5	selagcau	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	8	3	2	2	.	.	.	.	.
F	6	trichjas	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	1	.	1	3	2
F	6	trichobs	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	2	.	.	.	7	.	1
F	6	lindscul	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	3	2	1	.
F	6	cyathmol	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	.	1	.
F	6	diplacre	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	1	.	.	.	.
F	6	pronerub	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	12	5	.	.	.	.	.	.	.
F	6	teratlud	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	8	.	.	.	5	.
F	6	lindsrep	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	1
F	6	lindsdiv	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	1	.
F	6	pronegla	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	13	.	.	.	.	.	.	.
F	6	teratrot	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.
F	6	mesopmot	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	.	.	.	.
F	6	lindspar	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.

In addition to the 7 species for which the data from rubber plantation plots and jungle rubber plots were lumped, models were based only on rubber plantation plots for 4 species and only on jungle rubber plots for 12 species. For 6 species I modeled frequencies in both rubber plantation plots and jungle rubber plots (2 models per species). Results of the modeling are in Table 4.6.

Different HOF models were found for species that were similar ecologically and were placed in the same group, see Figures 4.8–12. Frequency values on which Figures 4.8–12 are based are given in Table 4.4.

Species in group 1 (Figure 4.8) have in common that they were almost exclusively found in rubber plantation plots. The ages of the plantations in which they were found differ however. *Helminthostachys zeylanica* is mostly an early species, whereas *Pteridium caudatum* and *Cyathea* sp.2 were found in plantations ranging in age from 8–14 and 13–17 years old, respectively. For *Adiantum latifolium* there appeared to be no relation with the age of the plantation.

Frequencies of all four species in group 2 (Figure 4.9) were on average higher in rubber plantation plots than in jungle rubber plots. In rubber plantations, frequencies were generally higher in older plantations than in younger plantations. *Nephrolepis biserrata* and *Stenochlaena palustris* often dominated the undergrowth of older rubber plantations. In jungle rubber gardens, *Blechnum orientale* and *Microlepia speluncae* occurred with low frequencies, and only in young jungle rubber. *Nephrolepis biserrata* was found in almost all jungle rubber gardens, but with much higher frequencies in young jungle rubber than in older gardens. *Stenochlaena palustris* was also common in jungle rubber; its frequencies did not change with the age of the garden. Frequencies of all four species were on average higher in rubber plantation plots than in jungle rubber plots. In rubber plantations, frequencies were generally higher in older plantations than in younger plantations.

Table 4.5 Results of tests for equality of means and variances of frequency values in rubber plantation (PL) plots and jungle rubber (JR) plots. Results are listed only for the seven species for which no significant differences were found.

Species name	Levene's test for equality of variances		t-test for equality of means (df = 19)		Mean in PL plots (N = 12)	Mean in JR plots (N = 9)
	F	Sig.	t	Sig. (2-tailed)		
Dicranopteris linearis var. *linearis*	0.02	0.89	-1.17	0.26	5.42	3.00
Asplenium pellucidum	0.23	0.64	0.75	0.46	1.92	3.11
Lygodium microphyllum	0.81	0.38	-0.51	0.61	5.25	4.11
Lygodium flexuosum	0.14	0.72	-0.50	0.62	3.08	2.11
Lygodium salicifolium	1.28	0.27	1.30	0.21	3.92	7.00
Lindsaea ensifolia	0.63	0.44	-0.26	0.80	9.17	8.56
Blechnum finlaysonianum	0.23	0.64	0.56	0.58	1.25	1.78

Table 4.6 Results of modeling of 29 species using a set of 5 models proposed by Huisman *et al*. (1993). Modeling was based on frequency data from rubber plantation plots (PL; N = 17), jungle rubber plots (JR; N = 23) or the combination of both (PL+JR; N = 40). Species were previously classified based on literature as 'forest species' (F) or 'non-forest species' (NF), see chapter 3, and are grouped in this chapter into 5 groups (see text).

Species name	Data used	HOF model	Parameter values	R^2	Literat. class.	Group
Helminthostachys zeylanica L. Hook.	PL	II	a = -6.79 b = 1.31	0.92	NF	1
Pteridium caudatum (L.) Maxon subsp. *yarrabense* (Domin) Parris	PL	IV	a = -35.96 b = 3.19 c = 28.92	0.44	NF	1
Cyathea sp.2	PL	IV	a = 144.44 b = -11.03 c = -154.11	0.84	not classified	1
Adiantum latifolium Lam.	PL	I	mean = 1.18		NF	1
Blechnum orientale L.	PL JR	I IV	mean = 2.82 a = -19.66 b = 0.80 c = 19.47	 0.81	NF	2
Microlepia speluncae (L.) Moore	PL JR	I II	mean = 5.47 a = 1.54 b = 0.07	 0.20	NF	2
Nephrolepis biserrata (Sw.) Schott	PL JR	II II	a = 1.82 b = -0.40 a = -4.92 b = 0.21	0.43 0.81	NF	2
Stenochlaena palustris (Burm.) Bedd.	PL JR	II I	a = 2.88 b = -0.34 mean = 7.04	0.51	NF	2
Dicranopteris linearis (Burm. f.) Underw. var. *linearis*	PL+JR	III	a = -163.06 b = 5.39 c = 0.97	0.24	NF	3
Asplenium pellucidum Lam.	PL+JR	IV	a = -15.55 b = 1.03 c = 15.04	0.28	F	3
Lygodium microphyllum (Cav.) R.Br.	PL+JR	II	a = 0.23 b = 0.06	0.19	NF	3
Lygodium flexuosum (L.) Sw.	PL+JR	II	a = -2.53 b = 0.36	0.40	NF	3
Christella subpubescens (Bl.) Holtt.	JR	I	mean = 1.39		NF	3
Lygodium salicifolium Presl	PL+JR	II	a = 0.17 b = 0.04	0.11	NF	3
Pronephrium triphyllum (Sw.) Holtt.	JR	V	a = -1.79 b = 0.18 c = 136.00 d = -7.72	0.39	NF	3
Selaginella willdenowii (Desv.) Baker	JR	I	mean = 3.22		NF	4

Table 4.6 Continued

Species name	Data used	HOF model	Parameter values	R^2	Literat. class.	Group
Lygodium circinnatum (Burm. f.) Sw.	JR	I	mean = 3.00		F	4
Dicranopteris linearis (Burm. f.) Underw. var. *subpectinata* (Christ.) Holtt.	JR	I	mean = 2.52		NF	4
Selaginella intermedia (Bl.) Spring	JR	II	a = 5.52 b = -0.10	0.52	F	4
Lygodium longifolium (Willd.) Sw.	PL	IV	a = -20.46 b = 2.99 c = 17.64	0.43	NF	4
	JR	II	a = 2.11 b = -0.04	0.25		
Schizaea dichotoma (L.) Sm.	JR	I	mean = 0.35		F	4
Lindsaea ensifolia Swartz	PL+JR	I	mean = 8.43		NF	4
Taenitis blechnoides (Willd.) Sw.	PL	III	a = 29.39 b = -3.12 c = -0.46	0.66	F	5
	JR	I	mean = 13.57			
Blechnum finlaysonianum Hk. & Grev.	PL+JR	I	mean = 1.35		F	5
Tectaria singaporeana (Wall. ex Hk. & Gr.) Copel.	JR	I	mean = 2.87		F	5
Lindsaea doryphora Kramer	JR	IV	a = -19.78 b = 1.01 c = 18.06	0.87	F	5
Mesophlebion chlamydophorum (C.Chr.) Holtt.	JR	I	mean = 1.04		F	5
Tectaria barberi (Hk.) Copel.	JR	I	mean = 0.39		F	5
Schizaea digitata (L.) Sw.	JR	I	mean = 2.00		F	5

Nephrolepis biserrata and *Stenochlaena palustris* often dominated the undergrowth of older rubber plantations. In jungle rubber plots, *Blechnum orientale* and *Microlepia speluncae* occurred with low frequencies, and only in young jungle rubber. *Nephrolepis biserrata* was found in almost all jungle rubber plots, but with much higher frequencies in young jungle rubber than in older plots. *Stenochlaena palustris* was also common in jungle rubber; its frequencies did not change with the age of the plot.

Group 3 (Figure 4.10) contains species that were commonly found in rubber plantations and, mostly young, jungle rubber. For five of the species in this group I found comparable frequency values in rubber plantations and young jungle rubber plots of similar age. The absence of some of those common species from older jungle rubber plots is striking. *Lygodium salicifolium* and *Pronephrium triphyllum* were found also in older jungle rubber plots, with *L. salicifolium* having lower frequencies than in younger jungle rubber plots. None of the species was found in primary forest.

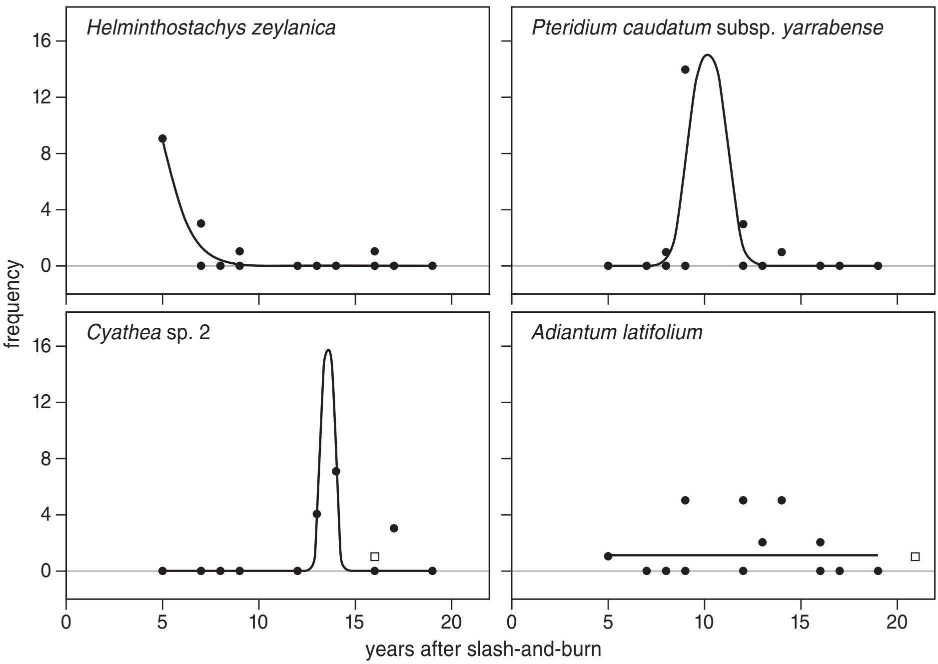

Figure 4.8 Modeled species of group 1: species found only or predominantly in rubber plantations. Graphs (solid lines) based on frequencies in rubber plantation plots (filled dots). Presence of the species in jungle rubber plots indicated by open squares.

Group 4 (Figure 4.11) consists of jungle rubber species and contains both early and late successional species. *Selaginella willdenowii* and *Lygodium circinnatum* were found predominantly in young jungle rubber, whereas *Schizaea dichotoma* was found only in old jungle rubber. *Selaginella intermedia* and *Lygodium longifolium* were found with higher frequencies in old jungle rubber than in rubber plantations, young jungle rubber or primary forest.

All species in group 5 (Figure 4.12) were found in jungle rubber and in primary forest, but only two, *Taenitis blechnoides* and *Blechnum finlaysonianum*, were also commonly found in (older) rubber plantations (although with lower frequencies). Frequencies found for *Taenitis blechnoides* in jungle rubber plots and primary forest plots were similar, and were higher than frequencies in rubber plantation plots. For *Blechnum finlaysonianum*, frequencies found in the three land use types differed little, and there appeared to be no relation with the age of the plot. *Tectaria singaporeana*, *Lindsaea doryphora*, *Mesophlebion chlamydophorum* and *Tectaria barberi* occurred in only one or a few rubber plantation plots. Their frequencies in jungle rubber plots did not seem to show a relation with age. *Schizaea digitata* was not found in rubber plantations. Frequencies found in primary forest plots were close to frequencies in jungle rubber plots for all modeled species in this group.

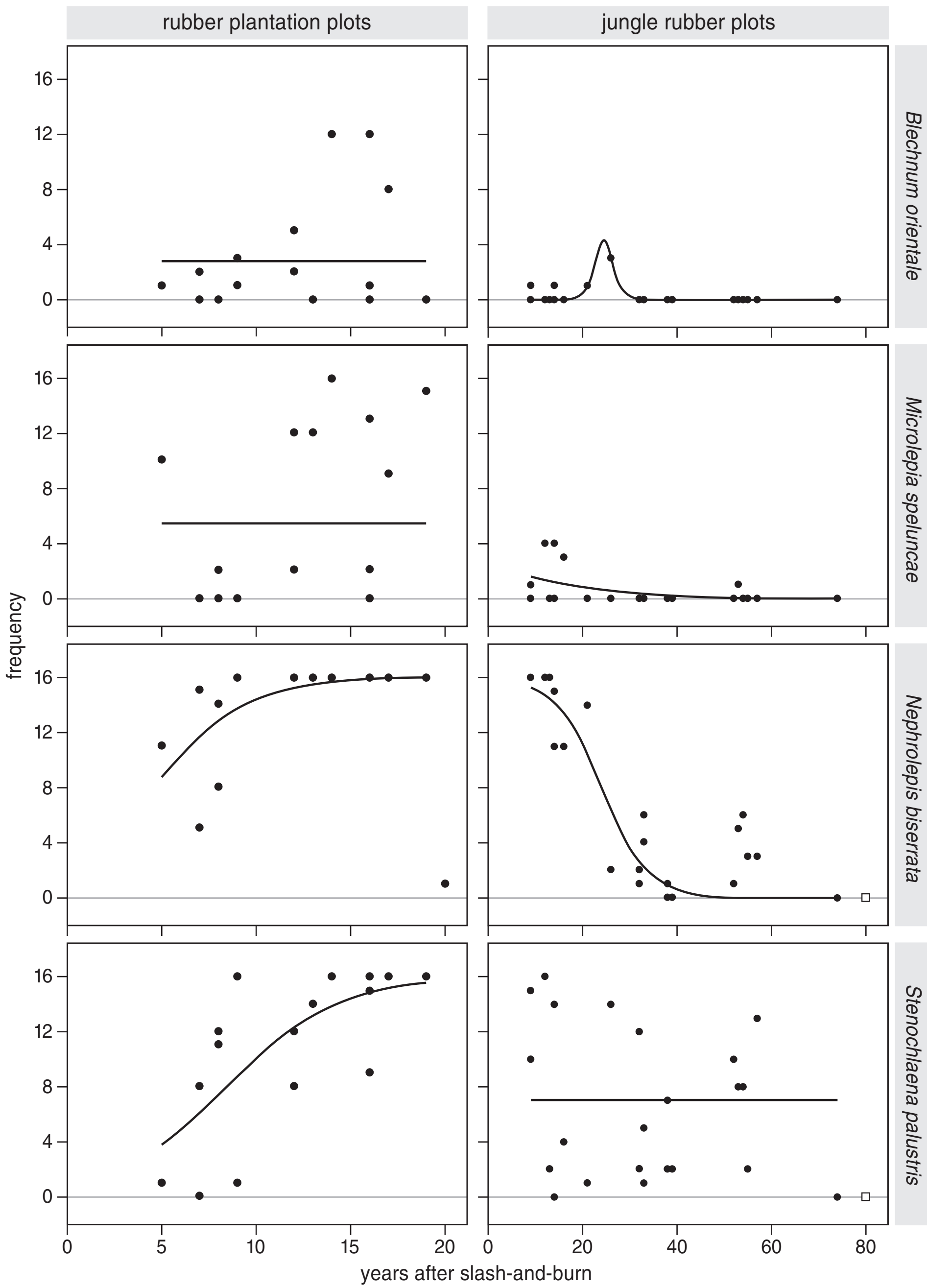

Figure 4.9 Modeled species of group 2: species found more in rubber plantations than in jungle rubber, and rarely or not in primary forest. Graphs (solid lines) based on frequencies in rubber plantation plots (filled dots, left graphs) or jungle rubber plots (filled dots, right graphs). Average frequency in 11 primary forest plots indicated by open squares (means and their standard errors).

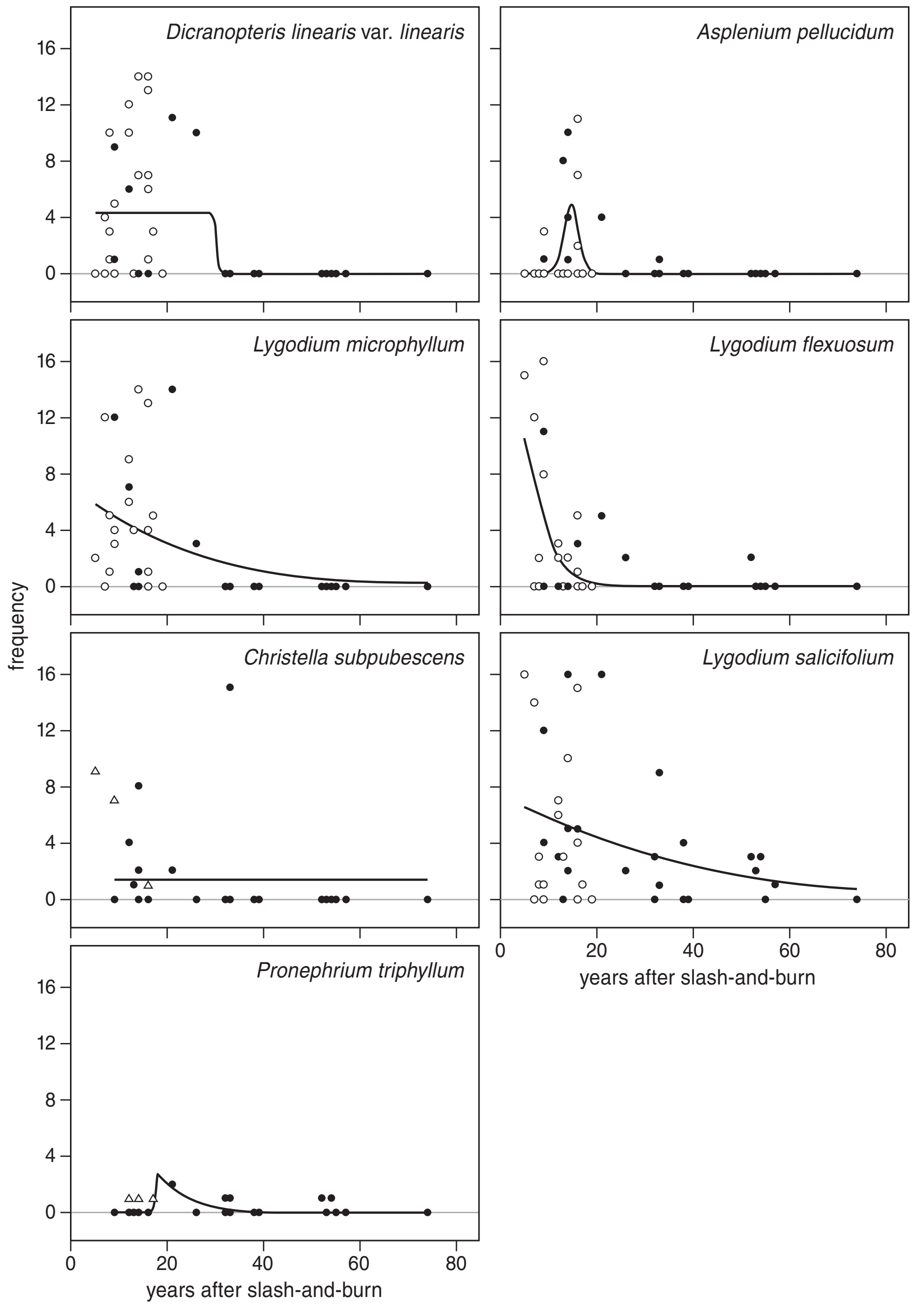

Figure 4.10 Modeled species of group 3: species found in rubber plantations and jungle rubber, not in primary forest. For *Dicranopteris*, *Asplenium* and 3 *Lygodium* species, graphs (solid lines) are based on frequencies in both rubber plantation plots (open dots) and jungle rubber plots (filled dots). For *Christella* and *Pronephrium* species, graphs are based on frequencies in jungle rubber plots only, while presence in rubber plantation plots is indicated by open triangles.

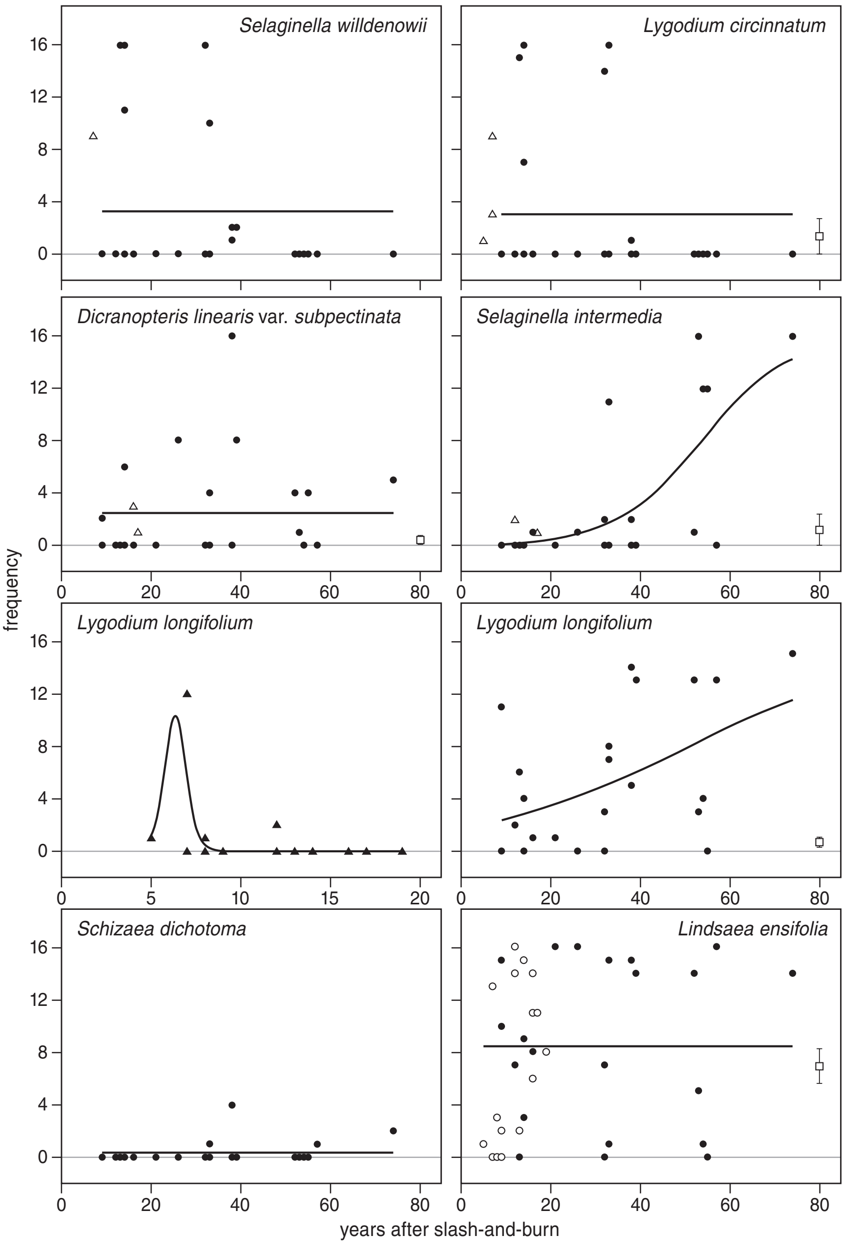

Figure 4.11 Modeled species of group 4: species found mostly in jungle rubber, less or not in rubber plantations and primary forest. For the *Selaginella*, *Dicranopteris* and *Schizaea* species, and *Lygodium circinnatum*, graphs (solid lines) are based on frequencies in jungle rubber plots only, while presence in rubber plantation plots is indicated by open triangles. For *Lygodium longifolium*, graphs are based on frequencies in rubber plantation plots (filled triangles, left graph) or jungle rubber plots (filled dots, right graph). For *Lindsaea ensifolia*, the graph is based on frequencies in both rubber plantation plots (open dots) and jungle rubber plots (filled dots). Average frequency in 11 primary forest plots indicated by open squares (means and their standard errors).

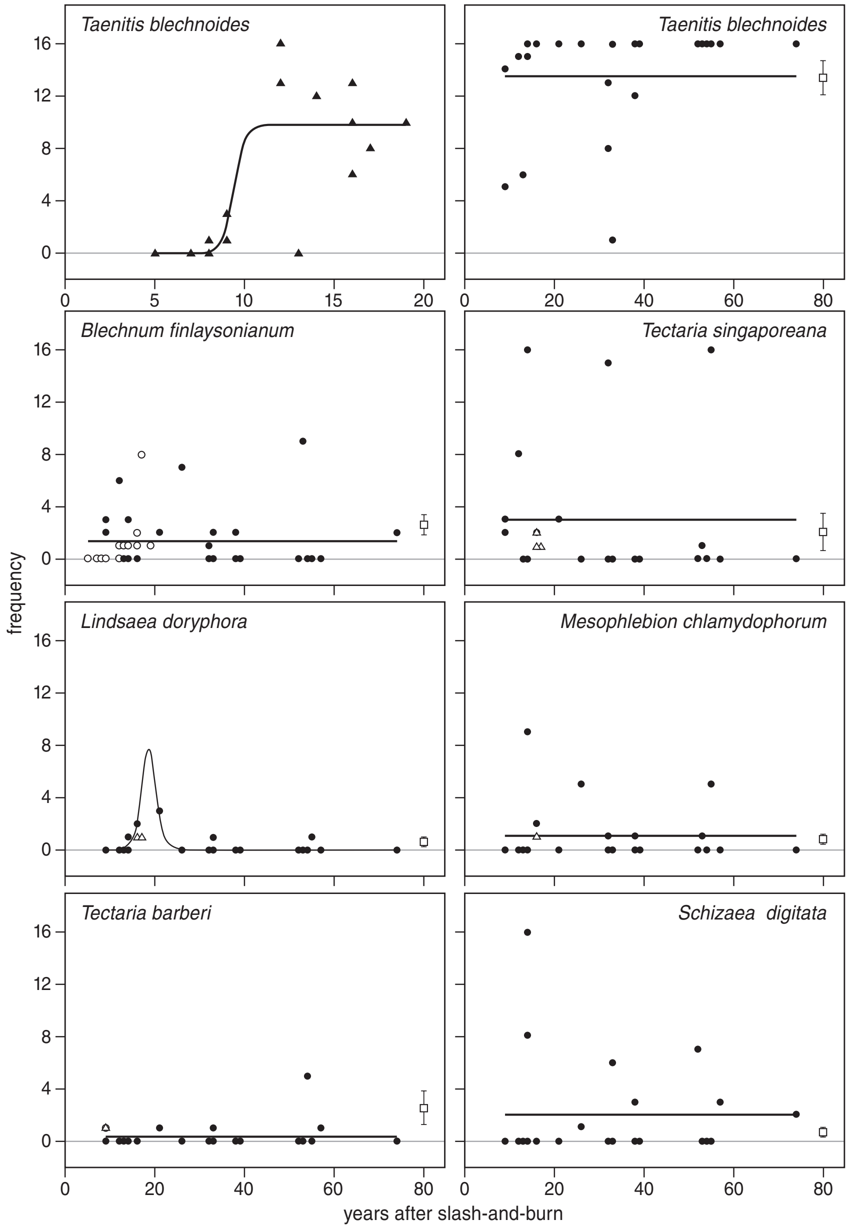

Figure 4.12 Modeled species of group 5: species found in jungle rubber and primary forest, and less or not in rubber plantations. Graphs (solid lines) for *Taenitis blechnoides* based on frequencies in rubber plantation plots (filled triangles, left graph) or jungle rubber plots (filled dots, right graph). Graph for *Blechnum finlaysonianum* based on frequencies in both rubber plantation plots (open dots) and jungle rubber plots (filled dots). Graphs for *Tectaria*, *Lindsaea*, *Mesophlebion* and *Schizaea* species based on frequencies in jungle rubber plots only, while presence in rubber plantation plots is indicated by open triangles. Average frequency in 11 primary forest plots indicated by open squares (means and their standard errors).

4.4.4 Successional patterns in land use types

Rubber plantations contained mostly species from groups 1, 2 and 3, and to a lesser extent from groups 4 and 5, while jungle rubber contained mostly species from groups 2, 3, 4 and 5. Primary forest contained mostly species from groups 4, 5 and 6.

Change in species composition with age was more pronounced in jungle rubber than in rubber plantations. With increasing age of jungle rubber plots, species of groups 2 and 3 became generally less abundant, especially after about 30 years of age, when some species disappeared altogether. A few species of group 4 became less abundant while others became more abundant with age of jungle rubber. The species of group 5 that were common in the dataset approached the average abundance found in primary forest with increasing age of jungle rubber. The less common species of group 5 were found sporadically in jungle rubber and were more abundant in primary forest.

In rubber plantations, some of the common species of group 5 appeared in older plantations, but with lower abundance than in jungle rubber plots. Older rubber plantations were increasingly dominated by two ground-covering species of group 2.

4.5 Discussion

4.5.1 Species classification

In Chapter 3, terrestrial pteridophyte species were classified *a priori*, based on information from the literature about their ecology. Two groups were made based on light requirements as described in the literature, while for about a quarter of the species (those preferring light shade) also the preferred habitat as described in the literature was taken into account. The groups were arbitrarily named 'forest species' and 'non-forest species' (see Chapter 3 for details). The classification was entirely based on information from outside the current research project, without taking data of this study into account. This was done for two reasons: (i) because it provided for a more or less objective grouping that might distinguish species' conservation value in a major land use change process, and (ii) because for most species, the literature is based on many records of the species (often herbarium vouchers) collected over a long period of time and over a large geographical area, whereas the dataset of this study contains many species that were found only in one or a few of the plots.

The species groups distinguished in the current chapter were based on the dataset. Presence of species in land use types was taken into account, as well as patterns of species abundance, expressed as frequency values in relation to the age of rubber plantations and jungle rubber agroforests. Depending on research aims, both types of classification may be useful tools. Whereas the literature-based classification into two groups is an approach that may be widely applicable for biodiversity and succession studies, the presented classification of species into six groups based on field data provided a useful structure for a more detailed understanding of the effects of management-related disturbance and succession processes in specific land use types.

In this section, I discuss the ecology of the main species in each group, using literature references and field observations, to better characterize those species and groups with respect to their ecology, and to evaluate the consistency of the data with the classification in Chapter 3.

Group 1. Species found only or predominantly in rubber plantations.
Most of the species in this group were classified as 'non-forest species'. *Helminthostachys zeylanica* can be found "near villages" and "never occurs in primitive high forest" (Holttum 1966). I found the species also in moist riverside grassland trampled by cattle.

Plants of *Pteridium caudatum* subsp. *yarrabense* "form thickets in open places" (Holttum 1966). Spores germinate nearly always in newly exposed open virgin habitats such as fire damaged sites or after forest logging, but never in closed vegetation including its own canopy (De Winter and Amoroso 2003). I found *Pteridium caudatum* also in recently burned fields and along roadsides, especially recently opened roads such as logging roads. It should be noted that modeling of this particular species with respect to the age of plots may not be of great use, as it is the one species farmers told us they actively eradicate, by digging out the rhizomes, when they see it in their rubber agroforest or plantation. The two rubber plantations where I found it to flourish both had absentee owners living far from the plantation.

Adiantum latifolium is an introduced species from Central and South America. It grows "profusely among the undergrowth of rubber plantations. In Singapore, it is invading the primary rainforest…" (Wee 1997). The only species attributed to group 1 and classified as a 'forest species' in Chapter 3 is *Pleocnemia irregularis*. Holttum (1974) writes that "[*Pleocnemia*] plants mostly grow in somewhat open places in forest, not in the deepest shade, often on sloping ground", while according to Piggott (1988) it is "common in light or partial shade in the lowlands, often occurring in plantations, and on the edge of forest in the hills, particularly on the inner corners of winding roads". According to De Winter and Amoroso (2003) this species "tolerates drier conditions than many other terrestrial forest ferns". I found *P. irregularis* outside the research area growing quite abundantly on a slope in an old jungle rubber agroforest near Muara Buat, an area with steep slopes in the foothills of the Barisan range. It may be that the species is relatively rare in the research area, which lacks such steep slopes, and that the few individuals found in the rubber plantation plots do not reflect its general ecological preference.

Group 2. Species found more in rubber plantations than in jungle rubber, and rarely or not in primary forest. As in group 1, most of the species in this group were classified as 'non-forest species'.
Holttum (1966) describes *Blechnum orientale* as "a sun-fern" and as "one of the commonest ferns in open places, never growing in shade", while De Winter and Amoroso (2003) state that "*B. orientale* is often a primary coloniser after forest clearing and fire and it sometimes becomes a dominant species after repeatedly being burnt". *Microlepia speluncae* "usually grows in places where it has shelter for its roots but a fairly bright light for its fronds" (Holttum 1966).

Nephrolepis biserrata grows "in open or lightly shaded places" and "can form dense thickets, spreading rapidly by means of its many long runners" (Holttum 1966). I found that this species was rather resistant to weed control, as it can resprout and form new runners quickly. *Stenochlaena palustris* is a sturdy plant with leathery leaves. It is "common everywhere in the lowlands, in open places and secondary forest, (…), never in shady primitive forest" (Holttum 1966). I found that *Nephrolepis biserrata* and *Stenochlaena palustris* often dominated older rubber plantations in terms of cover.

Pityrogramma calomelanos is an introduced species from tropical America, known to colonise post-eruption volcanic areas, disturbed ground and newly cleared ground (Holttum 1966, Spicer *et al.* 1985). I found that it is often one of the first fern species to appear on newly burned fields.

Sphaerostephanos heterocarpus was classified as a 'forest species' based on the very brief ecological note "In forest" by Holttum (1981). He notes, however, that there are a number of local forms of this species, which may imply that there may also be some variability in habitat preferences. *Selaginella plana* was also classified as a 'forest species', but too little data and literature on this species is available to describe its ecology well enough.

Group 3. Species found in rubber plantations and jungle rubber, and not in primary forest.
Dicranopteris linearis var. *linearis* was found only in young rubber plots, the oldest plot being 26 years, thus showing a different pattern than var. *subpectinata*, which was placed in group 4.

Asplenium pellucidum is the only species in this group that was classified as a 'forest species' in Chapter 3. That classification was based on the description by Backer and Posthumus ("in moist, shady forests") from 1939, since Holttum (1966) did not provide information on light preference of this species. However, the data and model results suggest that this species may be a 'non-forest' fern like the other modeled species in this group.

For the three closely related *Lygodium* species, *L. microphyllum*, *L. flexuosum* and *L. salicifolium*, I found similar patterns, with *L. salicifolium* also occurring in older jungle rubber.

Christella subpubescens occurs "in open places" (Piggott 1988) or "in lightly shaded places" (Holttum 1981). *Pronephrium triphyllum* occurs "in light shade, sometimes abundant under fruit trees or palms in villages" (Holttum 1981) and "never in the full shade of primitive forest" (Holttum 1966). This species is less common than the other species in the group, and the pattern is not as clear as for the other species.

Group 4. Species found mostly in jungle rubber, less or not in rubber plantations and primary forest.
Selaginella willdenowii was found mostly in young jungle rubber. According to Wong (1982), "*S. willdenowii*, by its rapid spread and clambering habit, is common along forest edges and soon becomes a smothering weed at many clearings and gaps. It can, however, grow lushly in darker conditions in the understorey of the forest". I did not, however, find this species inside any primary forest patch in the study area.

Group 4 has two closely related *Lygodium* species, *L. circinnatum* and *L. longifolium*. Holttum (1966) remarks in general of the genus *Lygodium* that its species "are very common in scrubby vegetation or secondary forest", and notes that *L. circinnatum* and *L. longifolium* "appear to need more shelter than [*L. microphyllum*] and [*L. flexuosum* and *L. salicifolium*], the last [three] being commonest in open country and often growing together". This observation agrees with the analogous grouping of the *Lygodium* species in groups 3 and 4. Holttum (1959) notes about the ecology of *L. circinnatum*: "In lightly shaded places in primary or secondary forest" and about *L. longifolium*: "Edges of forest, probably in more exposed places than *L. circinnatum*". Holttum (1966) adds for *L. circinnatum*: "in rather open places in primary and secondary forest in the lowlands, or on the edges of clearings. Young plants are common in some areas of primitive forest, but they usually do not grow large or bear fertile fronds in shady places". *L. circinnatum* was classified as a 'forest species' and *L. longifolium* as a 'non-forest species'. In this study, however, *L. circinnatum* was found mostly in young jungle rubber and in only 1 primary forest plot. *L. longifolium* was more abundant in older jungle rubber, and occurred in 4 primary forest plots.

Dicranopteris linearis var. *subpectinata* was classified as a 'non-forest species' based on information about the species *D. linearis* as a whole, because specific ecological information about the variety could not be found. However, the ecology of var. *linearis* (in group 3) and var. *subpectinata* in this group appear to be quite different. In addition to the data, I noticed in the field that plants of var. *linearis* generally grow larger and in denser thickets than plants of var. *subpectinata*, and that var. *linearis* grows in more disturbed and exposed places than var. *subpectinata*. I typically found var. *linearis* along or close to roadsides and in plantations, whereas var. *subpectinata* was usually found further away from roads, in jungle rubber agroforests and sometimes in primary forest. In De Winter and Amoroso (2003) it is noted that "*D*. *linearis* is a very variable species and many varieties have been described. Some of them are more distinct than others and should perhaps be considered as species."

Selaginella intermedia was classified as a 'forest species'. According to Wong (1982) this species has a "wide ecological amplitude". I found it mostly in (old) jungle rubber and primary forest. *Schizaea dichotoma* was found in older jungle rubber and not in primary forest, but is known to occur "sometimes in forest" (Holttum 1959). According to De Winter and Amoroso (2003) it is also commonly found in rubber plantations, but I did not find it there.

I found *Lindsaea ensifolia*, classified as a 'non-forest species', to be common and often abundant in all land use types. It was placed in this group because the average of the frequency values for jungle rubber plots was slightly higher than those for rubber plantation plots and primary forest plots. Kramer (1971) notes that *L. ensifolia* prefers "open, exposed situations, on banks, in natural and artificial grassland, and may then become somewhat weedy". For the other species that were assigned to this group, I have too few data to indicate whether they usually occur in young or old jungle rubber, and whether they are likely to occur in forest as well.

Group 5. Species found in jungle rubber and primary forest, and less or not in rubber plantations.
Species in this group were found with more or less similar frequency values in jungle rubber and primary forest plots. All species in this group were classified as 'forest species'.

Taenitis blechnoides and *Blechnum finlaysonianum* were also found in (older) rubber plantations, but their frequency values were higher in jungle rubber and primary forest plots. *Taenitis blechnoides* is "one of the commonest ferns of lowland and mid-mountain forest, occurring in drier places than most other terrestrial shade-ferns" (Holttum 1966). *Blechnum finlaysonianum* "is only found in shady forest, never in full sun like *B. orientale*" (Holttum 1966).

The other species in this group hardly occurred in rubber plantations. *Tectaria singaporeana* "is frequent in shady low country forest" (Holttum 1966). *Lindsaea doryphora* occurs "in moist to swampy forests" (Kramer 1971), whereas *Mesophlebion chlamydophorum* occurs "in lowland forest, especially freshwater swamp-forest" (Holttum 1981). *Tectaria barberi* "is fairly frequent in lowland primitive forest" (Holttum 1966). *Schizaea digitata* was not found in rubber plantations, whereas according to Holttum (1959) it occurs "in lightly shaded forest, rubber estates" and "in rather dry ground in sheltered places, often in rather open primary or secondary forest, or in rubber estates" (Holttum 1966).

Group 6. Species found only in primary forest.
All species in this group were classified as 'forest species' in Chapter 3. *Trichomanes javanicum* Bl. is mentioned as a 'shade-fern' ('heliophobic') by Backer and Posthumus (1939, p. 296), who also state that *Hymenophyllaceae* are very rarely found in secondary forest before this forest has developed to resemble the composition of primary forest (p. 312). In De Winter and Amoroso (2003), *Trichomanes javanicum* is called a rheophytic fern, however I have found this species in the primary forest plots well away from streams, indicating a shady and moist environment in the forest.

For most species in the dataset, the *a priori* classification turned out to be supported by field data. Probably misclassified were *Sphaerostephanos heterocarpus* (group 2) and *Asplenium pellucidum* (group 3), which may be better classified as 'non-forest species' rather than 'forest species', and *Lygodium longifolium* and *Dicranopteris linearis* var. *subpectinata* (both group 4), which may be better classified as 'forest species' rather than 'non-forest species'. Uncertainty about their correct classification remains for *Pleocnemia irregularis* (group 1), *Selaginella plana* (group 2) and *Lygodium circinnatum* (group 4), which were all classified as 'forest species'. The conclusions of Chapter 3 were not affected by those possible misclassifications.

Both Holttum (1966) and Backer and Posthumus (1939) dedicate some general remarks to a distinction between 'sun-ferns' and 'shade-ferns'. Holttum (1966) provides a short list of 'sun-ferns' but not of 'shade-ferns'. Species in the study that were explicitly mentioned by Holttum (1966) and/or Backer and Posthumus (1939) as 'sun-ferns' are listed in Table 4.7.

The terrestrial 'sun-ferns' are described by Holttum (1966) as "the common ferns of the open country-side which we see every day" (p. 20). When discussing 'shade-ferns' he mentions that there are a great number of terrestrial forest ferns (p. 21) and a small number of terrestrial ferns which are intermediate in character, growing in lightly shaded forest rather than in the full sun (p. 22).

I found that my data was in accordance with these observations by Holttum. The species in study plots that were classified in Chapter 3 as 'non-forest species' were usually more abundant than 'forest species', occurring on average with higher frequencies and in more plots than the 'forest species' did. Also, the total number of 'forest species' in the dataset was higher than the total number of 'non-forest species'.

It is questionable whether it is necessary in biodiversity studies to identify the "small number of ferns which are intermediate in character" (Holttum 1966) as a separate group. The mixture of 'non-forest species' and 'forest species' in the 'intermediate' group 4, growing in an 'intermediate' environment, may indicate that the classification of species into two groups rather than three was quite suitable for the kind of general interpretation of data for biodiversity studies at the community level, as was performed in Chapter 3. The approach of grouping species by light requirements, as applied in Chapter 3 and evaluated in this chapter, appears to be a useful method to study forest regeneration and to quantify the conservation value of agroforests, and may be widely applicable in tropical lowland rainforest areas.

4.5.2 Species and land use

In addition to the plot data, I noted that *Blechnum orientale*, *Microlepia speluncae*, *Nephrolepis biserrata*, *Stenochlaena palustris* and *Pityrogramma calomelanos* (all in group 2) were common species in farmer's fields in the first few years after slash-and-burn. I also observed those species and *Pteridium caudatum* (group 1) in Jambi in the first years of natural regeneration after forest fire, when ferns make up an important part of the vegetation biomass.

Table 4.7 Species in the study that are listed as 'sun-ferns' by Holttum (1966, pp. 20-21) or as 'heliophilous' by Backer and Posthumus (1939, p. 296).

'Sun-ferns' (current names)	Holttum 1966	Backer & Posthumus	Group	Literature classification
Pteridium caudatum subsp. *yarrabense*	X	X	1	NF
Blechnum orientale	X		2	NF
Nephrolepis biserrata	X		2	NF
Stenochlaena palustris	X		2	NF
Pityrogramma calomelanos	X	X	2	NF
Dicranopteris linearis	X	X	3 / 4	NF
Lygodium spp.	X		3 / 4	mostly NF
Lygodium microphyllum		X	3	NF
Lygodium flexuosum		X	3	NF
Lycopodium cernuum		X	4	NF
Cyathea contaminans		X	4	NF

Van Nieuwstadt (2002) found an average fern cover of 61% with *Blechnum orientale*, *Microlepia speluncae* and *Pteridium caudatum* as the most common fern species at 21 months after forest fire in East Kalimantan. De Winter and Amoroso (2003) note that "in a lowland rain forest in Sabah, *Nephrolepis biserrata* dominated the secondary vegetation in burnt plots two years after a forest fire in Borneo". Apparently, those species are able to establish quickly, and thrive in direct sunlight and the microclimatic extremes of open areas. In contrast with natural regeneration after forest fire, the early years of rubber plantations after slash-and-burn are characterised by a much reduced fern cover due to weeding and the use of herbicides, which is particularly intense when the rubber is still small. Abundance of *Blechnum orientale*, *Microlepia speluncae*, *Nephrolepis biserrata* and *Stenochlaena palustris* (group 2) increased with plantation age in the rubber plantation plots, even though shading by rubber trees also increased with age. The fact that those species, and *Adiantum latifolium* of group 1, actually do better in rubber plantations than in jungle rubber of the same age may indicate both their ability to cope with continued disturbance by management practices as well as a prevalence of more open, lighter and dryer conditions in rubber plantations, where shrubs, small trees and vines were mostly absent.

The species in group 3 that were common both in rubber plantations and in young jungle rubber apparently can cope with management-related disturbance irrespective of the level of disturbance. Although they do not seem to require such open, light conditions as preferred by species of groups 1 and 2, the light conditions have to be sufficient, as indicated by their absence from old jungle rubber plots.

Taenitis blechnoides (group 5), a common forest fern, was found with lower frequency values in rubber plantations than in jungle rubber and primary forest. This species either suffered from continued management-related disturbance, or needed more shady conditions than those present in rubber plantations. Frequency values of two species with a wide ecological range, *Blechnum finlaysonianum* (group 5) and *Lindsaea ensifolia* (group 4), were apparently quite independent from disturbance or light conditions.

Apart from direct effects of management practices, there may have been some indirect effects of land use on species composition in the plots as well. Although the original soil type under forest had been rather similar in the sampling area, changes in soil characteristics, such as texture and organic carbon content, resulting from (repeated) burning and cultivation may have altered growing conditions for pteridophytes. Slash-and-burn fires change soil mineralogy and texture (Ketterings *et al.* 2000). With regard to organic carbon content, Van Noordwijk *et al.* (1998) found that oxisols and ultisols in the area have an average organic carbon content of 3.2%, while the organic carbon content decreases in the order: primary forest > secondary forest > tree crop plantations by about 0.5% difference between land use types. Substantial improvement in soil fertility occurs only for a short period of time after the burn and may therefore not have affected species composition in the plots. Ketterings and Bigham (2000) found that within two months after the burn, exchangeable cations had decreased to pre-burn levels, whereas aluminium saturation had increased markedly.

Terrestrial pteridophytes may also have been affected by differences in properties of the litter layer, such as thickness, cover, and diversity of litter compounds. Plot position may have had some unknown effect on species composition, with rubber plots being positioned more on flat and slightly sloping land and on hilltops and forest plots more on hillside slopes.

4.5.3 Succession and the application of HOF models

The dataset does not cover the whole successional gradient. I sampled productive rubber systems, which means that I do not have data for the first years after slash-and-burn, and for the hundreds of years after the oldest jungle rubber has lost all rubber trees and restores to natural forest (which in the current land use situation is theoretical).

If one would think of the complete (theoretical) successional gradient in this study as starting with bare soil after slash-and-burn, continuing with succession in jungle rubber until beyond the end of a productive jungle rubber cycle, to end in primary forest, then one could distinguish two main successional patterns for terrestrial pteridophyte species with their expected HOF models: a pattern for transient species represented by (bell-shaped) models IV and V, and a pattern for climax species represented by the ascending forms of models II and III. Because of the incomplete gradient in the dataset, other HOF models can be expected to represent those two main successional patterns as well.

Transient species establish, increase in abundance and then decrease to a very low abundance (species may still appear in gaps in primary forest) or disappear. In the dataset, those species would be represented by models IV and V, but if the species establishes early (before the rubber starts to produce, i.e. outside the data range), they would also be represented by the decreasing forms of models II and III. The modeled species of groups 1, 2 and 3 all fit in this general picture.

In group 1, I found for two species a model IV and for one species a decreasing model II distribution. A model I distribution was found for *Adiantum latifolium*, but since the species was only found in one jungle rubber plot and not at all in forest, it conformed to the same general pattern.

For group 2, I regard the patterns for jungle rubber plots as most relevant for the general pattern of succession because of the longer age range. I found a model IV distribution for *Blechnum orientale* and decreasing model II distributions for *Microlepia speluncae* and *Nephrolepis biserrata. Nephrolepis biserrata* and *Stenochlaena palustris* still occur in (slightly) disturbed places in primary forest and in gaps, but only rarely and with very low abundance. For *Stenochlaena palustris* a model I distribution was found; probably this species will decrease in abundance only in a much later stage of the succession (outside the data range).

In group 3, there are species with model IV, model V, decreasing model II (three species), and decreasing model III distributions. For *Christella subpubescens* a model I distribution was found, but this is clearly an early species that disappears when jungle rubber gets older. Climax species establish, and then either increase in abundance, stay at the initial level of abundance, or decrease in abundance (but do not disappear). Either way, eventually the (non-zero) average abundance of the species in primary forest is reached. In the dataset, those species would be represented by model II or III distributions (increasing forms), or by model I or model V distributions.

For the modeled species of group 5, I found, based on jungle rubber plot data, model I distributions for six of the seven species, with the average frequency values in jungle rubber close to the average frequency values in primary forest plots for most species. The model IV distribution, that was statistically the best model for *Lindsaea doryphora*, does not provide a correct interpretation ecologically. *L. doryphora* is a rather rare species that is found in jungle rubber and primary forest alike, which would have been better represented by a model I or V distribution.

For the intermediary group 4, I found an increasing model II distribution for two species, and a model I distribution for five species, which would be consistent with expected patterns for climax species rather than transient species. However, the intermediary character of this group is supported by the fact that model I distributions in this group were found both for species that occurred mostly in young jungle rubber and for species that occurred mostly in old jungle rubber, as well as by the fact that for all species in this group the abundance in jungle rubber plots was higher than in primary forest plots.

Although the five HOF models do not directly translate to five successional patterns that could be found for terrestrial pteridophyte species with regard to secondary forest succession, in general the set of models was quite suitable to clarify abundance patterns for individual species with respect to plot age and management-related disturbance. However, not all models were equally useful. Model I accurately represented the abundance patterns for some species, for instance for species in group 5, while for other species the model did not add to the interpretation of patterns and acted more as a default model, such as for the species in group 4 that were either found in younger or in older jungle rubber plots. Model III distributions were only found twice and a model V distribution only once. This is due to the fact that these models are very similar in shape to models II and IV, respectively, but introduce one more parameter to be weighed against a possible better fit. For this study, including models III and V did not add much, except for the pattern of *Taenitis blechnoides* in rubber plantations (group 5).

Whereas modeling was useful to clarify abundance patterns, it provided little additional value for documenting age ranges of plots where individual species were found. The actual data provided more information than the models for some species, e.g. for *Blechnum orientale* in jungle rubber (group 2), which occurred earlier in succession than the model distribution suggests, and *Lindsaea doryphora* (group 5), which occurred both in young and old jungle rubber.

4.5.4 Indicator species

To conclude this chapter, I give a short overview of (groups of) species in the study that could be used as indicators. It should be noted that this is done within the limits of the sample, which means that flooded banks and edges of forest streams as well as micro-environments such as steep earth walls are excluded. I selected terrestrial pteridophyte species as potential indicators of forest disturbance and/or forest regeneration that showed clear abundance patterns in relation to disturbance and forest age.

Blechnum orientale, *Microlepia speluncae*, *Nephrolepis biserrata*, *Dicranopteris linearis* var. *linearis*, *Asplenium pellucidum*, *Lygodium microphyllum* and *Lygodium flexuosum* indicate highly to moderately disturbed early successional situations. These species are all common in the Malaysian region and are easy to recognise. In chronosequence studies, decrease in abundance and disappearance of these species with age may indicate forest regeneration.

Nephrolepis biserrata may be particularly suitable to track restoration of forest after fire or slash-and-burn. This species was present over the full length of the successional gradients in rubber plantations and jungle rubber, as well as in forest after fire, with different abundance patterns. It was found to be very abundant in the most disturbed situations, such as burned forest in the first years after forest fire, newly planted fields after slash-and-burn, rubber plantations, and very young jungle rubber. Its abundance decreased rapidly in jungle rubber between 21 and 26 years of age, but the species remained present with intermediate abundance in all but a few jungle rubber plots. *N. biserrata* was rarely found in primary forest, and when it was present it was represented by a single small individual. This species can be expected to gradually disappear in older secondary forest.

Selaginella willdenowii and *Dicranopteris linearis* var. *subpectinata* are also easily recognisable species, and indicative of moderate disturbance associated with secondary forest succession.

Higher abundances of *Taenitis blechnoides* may point to relatively less disturbed situations when samples from different land use types, such as plantations and agroforests, are compared.

With the exception of *Blechnum finlaysonianum*, which is a species with a broad ecological range, presence of species of group 5 is indicative of (the restoration of) a forest environment. The number of such species found in disturbed forest samples relative to the number found in undisturbed forest samples could be a useful measure of forest restoration or of forest quality. The same can be said of the forest species of group 6.

While this study was performed in the peneplain of Jambi province in Sumatra, results may apply to the larger area of the uplands of the central peneplains of Sumatra, which have similar soil and climate conditions, as described by Scholz (1983). In addition, most of the pteridophyte species mentioned above as indicators of disturbance are widely distributed geographically, and may therefore be useful indicators in other lowland forest areas in the Malaysian region, such as Peninsular Malaysia and the island of Borneo.

Acknowledgements

Thanks to Ricardo Ibáñez and Rudy van Diggelen for advice on running HOF equations in SPSS and to Dr. P.H. Hovenkamp and Dr. H.P. Nooteboom of the National Herbarium of the Netherlands for checking species identifications.

Acronyms

P2WK = Proyek Pengembangan Wilayah Khusus (Special area development project)

NES/PIR = Nucleus Estate Smallholders / Perkebunan Inti Rakyat

References

Backer, C.A., and Posthumus, O., 1939. Varenflora voor Java. Overzicht der op Java voorkomende varens en varenachtigen, hare verspreiding, oekologie en toepassingen. 's Lands Plantentuin, Buitenzorg, Java.

Chokkalingam, U., and De Jong, W., 2001. Secondary forest: a working definition and typology. International Forestry Review 3, 19-26.

De Winter, W.P. and Amoroso, V.B. (Editors), 2003. Plant Resources of South-East Asia No 15(2). Cryptogams: Ferns and fern allies. Backhuys Publishers, Leiden, The Netherlands.

Gouyon, A., De Foresta, H., and Levang, P., 1993. Does 'jungle rubber' deserve its name? An analysis of rubber agroforestry systems in southeast Sumatra. Agroforestry Systems 22, 181-206.

Holttum, R.E., 1959. Gleicheniaceae. In: Van Steenis, C.G.G.J., Holttum, R.E. (Eds.), Flora Malesiana Ser. II Pteridophyta 1 (1). Martinus Nijhoff / Dr W. Junk Publishers, The Hague, pp. 1-36.

Holttum, R.E., 1966. Ferns of Malaya. Second Edition. Botanic Agroforests Singapore / Government Printing Office, Singapore.

Holttum, R.E., 1974. The fern-genus Pleocnemia. Kew Bull. 29[2], 341-357.

Holttum, R.E., 1981. Thelypteridaceae. In: Van Steenis, C.G.G.J., Holttum, R.E. (Eds.), Flora Malesiana Ser. II Pteridophyta 1(5). Martinus Nijhoff / Dr W. Junk Publishers, The Hague, pp. 331-560.

Huisman, J., Olff, H., Fresco, L.F.M., 1993. A hierarchical set of models for species response analysis. Journal of Vegetation Science 4, 37-46.

Ketterings, Q.M., Bigham, J.M., 2000. Soil color as an indicator of slash-and-burn fire severity and soil fertility in Sumatra, Indonesia. Soil Sci. Soc. Am. J. 64, 1826-1833.

Ketterings, Q.M., Bigham, J.M., Laperche, V., 2000. Changes in soil mineralogy and texture caused by slash-and-burn fires in Sumatra, Indonesia. Soil Sci. Soc. Am. J. 64, 1108-1117.

Kramer, K.U., 1971. Lindsaea group. In: Van Steenis, C.G.G.J., Holttum, R.E. (Eds.), Flora Malesiana Ser. II Pteridophyta 1(3). Martinus Nijhoff / Dr W. Junk Publishers, The Hague, pp. 177-254.

Laumonier, Y., 1997. The vegetation and physiography of Sumatra. Geobotany 22. Kluwer, Dordrecht.

Mueller-Dombois, D., and Ellenberg, H., 1974. The count-plot method and plotless sampling techniques. Chapter 7, pp. 93-135 in: Aims and methods of vegetation ecology. John Wiley & Sons, New York.

Munsell color, 1994. Munsell soil color charts. Revised edition. Macbeth Division of Kollmorgen Instruments Corporation, New Windsor, NY, USA.

Oldeman, L.R., Las, I., and Darwis, S.N., 1979. An agroclimatic map of Sumatra. Contr. Centr. Res. Inst. Agric. Bogor 52, 1-35.

Piggot, A.G., and Piggot, C.J., 1988. Ferns of Malaysia in colour. Tropical Press Sdn. Bhd., Kuala Lumpur, Malaysia.

Scholz, U., 1983. The natural regions of Sumatra and their agricultural production pattern. A regional analysis. Volume 1. Bogor, Central Research Institute for Food Crops (CRIFC), AARD, Ministry of Agriculture, Republic of Indonesia.

Spicer, R.A., Burnham, R.J., Grant, P., Glicken, H., 1985. Pityrogramma calomelanos, the primary, post-eruption colonizer of Volcán Chichonal, Chiapas, Mexico. Am. Fern J. 75[1], 1-5.

Tomich, T.P., Van Noordwijk, M., Budidarsono, S., Gillison, A., Kusumanto, T., Murdiyarso, D., Stolle, F., Fagi, A.M., 1998. Alternatives to Slash-and-Burn in Indonesia. Summary report & synthesis of phase II. ASB-Indonesia Report no. 8, ICRAF S.E. Asia, Bogor, Indonesia.

Torquebiau, E.F., 1988. Photosynthetically active radiation environment, patch dynamics and architecture in a tropical rainforest in Sumatra. Aust. J. Plant Physiol. 15, 327-342.

Van Nieuwstadt, M.G.L., 2002. Trial by fire. Postfire development of a tropical Dipterocarp forest. PhD thesis, Universiteit Utrecht, The Netherlands.

Van Noordwijk, M., Murdiyarso, D., Hairiah, K., Wasrin, U.R., Rachman, A., Tomich, T.P., 1998. Forest soils under alternatives to slash-and-burn agriculture in Sumatra, Indonesia. In: Schulte, A., Ruhiyat, D. (Eds.), Soils of tropical forest ecosystems: characteristics, ecology and management. Springer-Verlag, Berlin, pp. 175-185.

Wahyunto, Subardja, D., Puksi, D.S., Rochman, A., Paidi, R., Wahyu, W.M., Hidayat, A., Dai, J., 1990. Explanatory booklet of the land unit and soil map of the Muara Bungo sheet (0914), Sumatra, scale 1:250.000. Centre for Soil and Agroclimate Research, Bogor, Indonesia.

Wee, Y.C., 1997. Ferns of the tropics. Times Editions, Singapore.

Whitten, A.J., Damanik, S.J., Anwar, J., Hisyam, N., 1987. The ecology of Sumatra. Gadjah Mada University Press, Yogyakarta, Indonesia.

Wong, K.M., 1982. Critical observations on Peninsular Malaysian Selaginella. Gard. Bull. (Singapore) 35[2], 107-135.

Chapter 5

Plant and bird diversity in rubber agroforests in the lowlands of Sumatra, Indonesia

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Published in Agroforestry Systems 70 (2007), 217-242.

Abstract

Plant and bird diversity in the Indonesian jungle rubber agroforestry system was compared to that in primary forest and rubber plantations by integrating new and existing data from a lowland rain forest area in Sumatra. Jungle rubber gardens are low-input rubber (*Hevea brasiliensis*) agroforests that structurally resemble secondary forest and in which wild species are tolerated by the farmer. As primary forests have almost completely disappeared from the lowlands of the Sumatra peneplain, our aim was to assess the contribution of jungle rubber as a land use type to the conservation of plant and bird species, especially those that are associated with the forest interior of primary and old secondary forest. Species-accumulation curves were compiled for terrestrial and epiphytic pteridophytes, trees and birds, and for subsets of 'forest species' of terrestrial pteridophytes and birds. Comparing jungle rubber and primary forest, groups differed in relative species richness patterns. Species richness in jungle rubber was slightly higher (terrestrial pteridophytes), similar (birds) or lower (epiphytic pteridophytes, trees, vascular plants as a whole) than in primary forest. For subsets of 'forest species' of terrestrial pteridophytes and birds, species richness in jungle rubber was lower than in primary forest. For all groups, species richness in jungle rubber was generally higher than in rubber plantations. Although species conservation in jungle rubber is limited by management practices and by a slash-and-burn cycle for replanting of about 40 years, this forest-like land use does support species diversity in an impoverished landscape increasingly dominated by monoculture plantations.

5.1 Introduction

5.1.1 Rubber agroforest as a disturbed forest type

In areas undergoing rapid land use change such as the lowlands of Sumatra, where undisturbed lowland forest has almost completely disappeared (Lambert and Collar 2002), the question whether at least some of the lowland rainforest species can survive in disturbed forest types has become important. The potential significance of agricultural production systems for biodiversity conservation is stressed by nature conservation agencies and the international research community (WRI 1992, pp. 110–115, 128, and 130; Halladay and Gilmour 1995, Collins and Qualset 1999, Siebert 2002, García-Fernández *et al.* 2003, Garrity 2004, Schroth 2004).

Most primary forests and logged forests in the lowlands of Sumatra have been converted since the 1970s to large-scale monoculture plantations (oil palm, rubber, industrial timber) as well as transmigration sites (World Bank 2001). Smallholder rubber agroforest, also called 'jungle rubber' (Gouyon *et al.* 1993), on the other hand is a major land use type in the Sumatran lowlands that has existed since the beginning of the 20th century. With current land use changes, it may become the most extensive forest-like vegetation type in the area.

Even though these agroforests are planted and owned by a farmer, the component of spontaneous secondary vegetation in these agroforests is large enough to regard them as a type of disturbed or secondary forest vegetation in the context of biodiversity research. Jungle rubber gardens are usually weeded for the first 2–3 years after slash-and-burn, when rice and vegetables are grown together with newly planted rubber tree seedlings. No herbicides or fertilisers are used. After the first few years, most wild species that colonise the gardens are allowed to grow with the rubber trees, and a complex forest-like vegetation develops. In mature gardens, management is usually limited to maintaining paths between rubber trees to allow for tapping. Jungle rubber gardens are on average replanted after about 40 years, but some gardens are maintained to an age of 70–80 years. Gouyon *et al.* (1993) found that two older jungle rubber gardens (35–40 years old and 40–45 years old) were structurally similar to secondary forest. Older jungle rubber gardens (>30 years old) can reach a height of 20–40 m in the Jambi lowlands, compared to 43–60 m for primary forests in the same area (H. Beukema, unpublished data). The percentage of trees that are rubber trees is variable, and declines with the age of the garden. On average, about 40–50 % of the trees in mature gardens are rubber trees (Hardiwinoto *et al.* 1999).

As a land use type, jungle rubber will most probably remain important. Smallholder rubber covered about 530,000 ha in Jambi province in 1996 (Dinas Perkebunan Jambi 1998, p. 27) and almost three million hectares in Indonesia in 1997 (Ministry of Forestry and Estate Crops 1998). Economic prospects for rubber on the world market are positive (Smit and Vogelvang 1997; Burger and Smit 1998, 2000) and production by smallholders is still profitable (Levang *et al.* 1999, Suyanto *et al.* 2001).

Michon and De Foresta (1992) drew attention to the issue of complex agroforestry systems and conservation of biological diversity in Indonesia. They pleaded for "assessment of existing and potential capacity of agricultural ecosystems to preserve biological diversity" and presented inventory data on vegetation of multistrata agroforestry systems in Sumatra. Their early conclusion was that agroforests cannot replace protected forest reserves but can "contribute to maintaining in the landscape a useful and diversified forest ecosystem from which the peasant is not excluded". However, they also remarked at the time that "reliable comparisons of biodiversity levels between forest and agroforestry ecosystems have still to be done". In this paper we summarise such comparisons, combining plant and bird data from published papers, research reports, and our own research in Sumatra.

The aims of this study are:
- To compare diversity patterns of plants and birds, as well as subgroups of plants such as pteridophytes and trees, in three land use types: primary forest, jungle rubber, and rubber plantations, in the lowlands of Sumatra.
- To assess the contribution of jungle rubber as a land use type to the conservation of plant and bird species that are associated with the forest interior of primary and old secondary forest.

5.1.2 Sampling for biodiversity research in jungle rubber
Sampling in jungle rubber is complicated by the internal variability of this land use type. It is a cultivation system of smallholder farmers who usually own several small and scattered rubber gardens of different ages and varying in size from less than one to a few hectares. This results in a rubber landscape that is a mosaic of small gardens of different ages, rubber densities and management intensities. Because slash-and-burn is used to establish rubber gardens, 'wild' species have to establish themselves anew by invasion from surrounding areas, or regenerate from the seedbank or sprouting stumps. Succession starts from burned and weeded fields and is influenced by source populations in surrounding areas, by selective activities of farmers and by the cultivation history of the garden. The resulting variety within the jungle rubber land use type cannot be fully captured by data collected in a single or a few gardens. Sampling a larger set of gardens or a transect that more or less represents the land use type as a whole is required to study biodiversity in jungle rubber.

Scale-dependency of effects of disturbance is another complicating factor for biodiversity research in jungle rubber. Scale effects are important in disturbance studies (Hill and Hamer 2004). Hamer and Hill (2000) investigated the effect of the spatial scale at which Lepidoptera communities were sampled, and found that "disturbance had opposite effects on diversity at large and small scales: as scale decreased, the probability of a positive effect of disturbance on diversity increased".

To account for the internal variability of the land use type and the scale-dependency of effects of disturbance, datasets should ideally be large and cover a large number of jungle rubber gardens. However, a practical problem that arises when sampling diverse groups in a range of gardens is the large number of specimen to be identified. For vascular plants, sampling of a single 0.02 ha plot in a jungle rubber garden already yielded more than 100 species (Gillison *et al.* 1999). The largest available dataset comparing forest and jungle rubber for vascular plants contains hundreds of species, for which more than 1000 herbarium specimen were analysed (Michon and De Foresta 1995), while its data for jungle rubber was collected in two gardens only.

Limiting sampling to particular subgroups, such as ferns or trees, allows for collection of data over a larger number of gardens. However, species richness patterns found for such subgroups may differ and the issue of representativeness needs to be addressed. For instance, we may assume that for the group of vascular plants as a whole, the general trend is most likely a decrease in species richness with disturbance from forest to jungle rubber to rubber plantation. However, different components or subgroups within the group of vascular plants would not necessarily have to conform to this trend. Speed of (re)colonisation and suitability of the rubber habitat will differ for different subgroups of plants.

5.1.3 Conservation of forest species in jungle rubber

Plant and bird species that are associated with the forest interior of primary and old secondary forest are most affected by habitat loss through large scale forest conversion in the Sumatran lowlands. To assess the contribution of jungle rubber to the conservation of those species that are most in need of protection, we need to look not just at total plant or bird species diversity in jungle rubber, but also at the relation of different groups of species to disturbed forest habitat and forest succession. The invasion of non-forest species or early-successional species may obscure our view on the reduction of true forest species with disturbance. For instance, species of terrestrial pteridophytes vary in their requirements for shade, and groups of 'forest species' and 'non-forest species' of terrestrial pteridophytes can be distinguished based on those requirements (Beukema and Van Noordwijk 2004). Epiphytes on the other hand are mostly related to old secondary forest and primary forest, as they depend on the development of tree trunks and branches for their habitat. Habitat requirements of birds have been studied well enough to allow for basic grouping of species by their main natural habitat in the Sumatran lowlands and their level of association with lowland forest.

Rapid assessment studies (Gillison 2000) have indicated that jungle rubber and other moderately disturbed types such as logged forest and old secondary forest 'score' rather high on total species richness. It is especially important to interpret those results in terms of ecological groups, and to investigate whether high species richness values found for jungle rubber could be due to invasion of non-forest species or to scale effects.

5.2 Methods

5.2.1 Study area

All data presented are from lowland areas (<150 m above sea level) in Sumatra. Most research was done in Jambi province and, across the northern provincial border of Jambi, in Riau province (Figure 5.1).

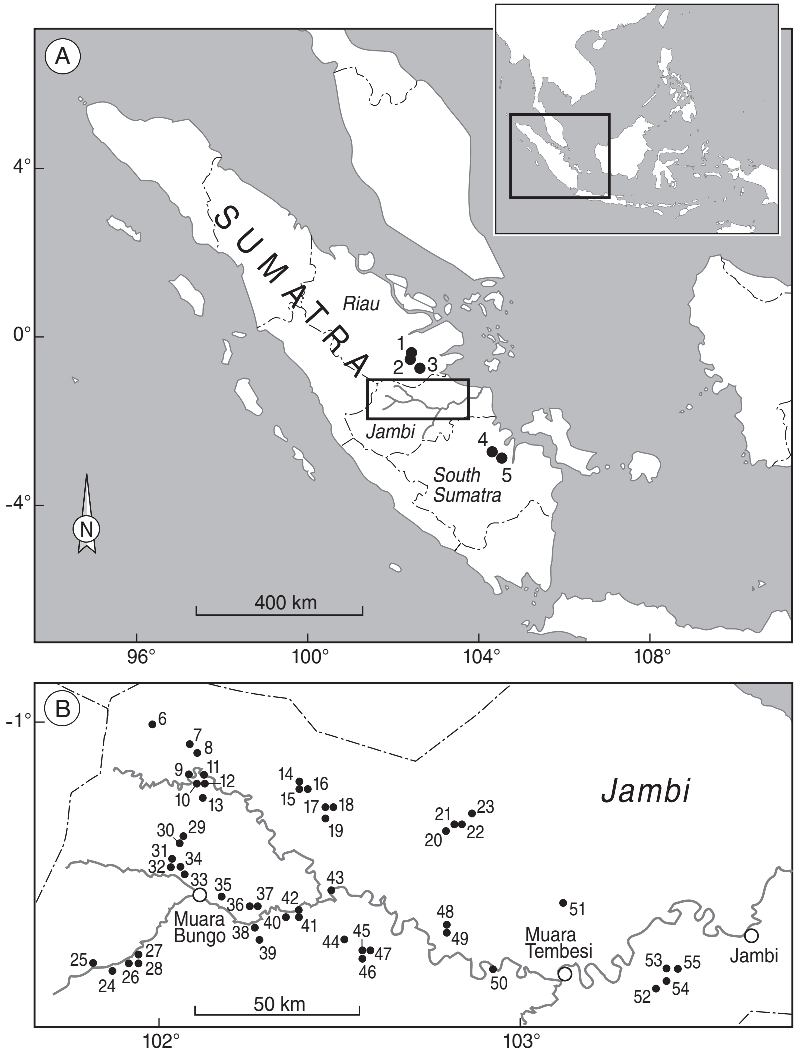


Figure 5.1 Research areas in the lowlands of Sumatra, Indonesia, in the provinces of Riau and South Sumatra (A) and Jambi (B). Riau: Sibabat Dua (1), Pangkalan Kasai (2), Talang Lakat/Sungai Akar (3); South Sumatra: Sukaraja (4), Sembawa Research Station (5). Jambi: Pasir Mayang (6–8), Teluk Cempako (9), Pancuran Gading (10), Dusun Tuo Ulu (11–13), Semambu (14–16), Muara Sekalo (17–19), Lubuk Kambing (20–23), Muara Buat (24), Rantau Pandan (25–28), Wiroto Agung (29, 30), Rimbo Bujang (31–33), Sarana Jaya (34), Babeko (35), Sepunggur (36, 37), Muara Kuamang (38, 39), Sungai Bungur (40), Sungai Tilan (41, 42), Semabu (43), Silva Gama (44), Pintas Tuo (45–47), Bukit Sari (48, 49), Sungai Puar (50), Rantaupuri (51), Batin (52), Muara Bulian (53, 54), Maro Sebo (55). Sampling by different researchers in forest (f), jungle rubber (j) and rubber plantation (p). Vascular plants: De Foresta 5p, 24j, 26f, 28j, Gillison *et al.* 7f, 8p, 10j. Pteridophytes: Beukema 7f, 8p, 9j, 11p, 12p, 13p, 14j, 15j, 16f, 17f, 18f, 19j, 20f, 21j, 22p, 23j, 29p, 30p, 31p, 32p, 33p, 34p, 35p, 35j, 39j, 40j, 41j, 42j, 43p, 44f, 48f, 49f, 50j, 52p, 53p, 54p, 55p. Trees: Laumonier 7f, Franken and Roos 6f, 51f, Vincent *et al.* 39j, Hardiwinoto *et al.* 24j, 27j, 28j, 36j, 37j, 38j, 39j, 45j, 46j, 47j, De Foresta 4j, Kheowvongsri 24j. Birds: Danielsen and Heegaard 1p, 2j, 3f, Jepson and Djarwadi 7f, 8p, 10j, Thiollay 25j.

Annual rainfall in the Jambi peneplain is about 3,000 mm per year. On average, there are 7–8 wet months (>200 mm rainfall / month) per year, and no months with less than 100 mm of rainfall. The driest months are from May to September. Yearly average minimum and maximum temperatures are 22.5 °C and 31.4 °C, respectively. The terrain is slightly undulating to flat, and soils are predominantly well-drained, acid oxisols with low fertility. Biophysical, socio-economical and historical aspects of land use, including jungle rubber, in central Sumatra are described in Gouyon *et al.* (1993), Sandbukt and Wiriadinata (1994), Van Noordwijk *et al.* (1995), Potter and Lee (1998), and Tomich *et al.* (1998). The 'forest' land use type in the datasets in this paper (indicated as 'forest' or 'primary forest') comprises old growth mixed Dipterocarp lowland rain forest (Laumonier 1997) without visible traces of timber cutting and without known history of logging or shifting cultivation, the only human use being limited collection of non-timber forest products and hunting.

Large areas of (mostly logged) forest still present in Jambi province during the sampling period (1990–1999) were located in the foothills of the Barisan Range to the west, bordering the Kerinci Seblat National Park, and in a belt of forest near the border with Riau province to the north, including the Bukit Tigapuluh Range (see also the maps in Potter and Lee 1998). In the more agricultural central and southern parts of the province, a few small fragments of primary forest as well as some larger fragments of logged forest remained at the time. Except for the small Pasir Mayang study area to the north, most primary forests in this study have since been logged or converted to other uses. Very little unlogged forest now remains in the area, and conversion of logged forest is still ongoing. A recent land use change study (Ekadinata *et al.* 2004; Ekadinata *et al.*, unpublished data) based on remote sensing images of Bungo district, in the western part of Jambi province, indicates a change in forest cover from 70% of the total area in 1973 to 51% in 1988 and 28% in 2002, with remaining forest cover mostly located at higher altitudes in the Barisan Range. Jungle rubber cover was 16% in 1973 and 17% in 1988, and down to 13% of the total area in 2002, while monoculture plantations (rubber and oilpalm) increased steadily, covering 6% in 1973, 23% in 1988, and 46% of Bungo district in 2002. About 16% of our sampling locations were located in Bungo district, which comprises a 4550 km^2 area or about 9.2% of Jambi province.

5.2.2 Datasets

All vascular plants

Two datasets were available for comparison of species richness of vascular plants in forest, jungle rubber and rubber plantations in Sumatra: one by De Foresta (unpublished corrections of data in De Foresta 1991 and Michon and De Foresta 1995) and one by Gillison *et al.* (1999). De Foresta sampled vascular plant species along 100 m line transects. One transect was sampled in forest and two transects in jungle rubber, in two different gardens, both 50–60 years old, in 1993. Mean size of jungle rubber gardens in the area (Muara Buat in Jambi) was about 1 ha (H. de Foresta, pers. comm.). One transect was sampled in a 20-year-old rubber plantation in 1991. Gillison *et al.* sampled vascular plant species in 40 m × 5 m (0.02 ha) plots. Two replicate plots per land use type were sampled in a patch of forest, a jungle rubber garden (age uncertain), and a 16-year-old rubber plantation, in 1997. All data were from Jambi province except for the rubber plantation transect by De Foresta, which was in South Sumatra province.

PTERIDOPHYTES

Terrestrial and epiphytic pteridophyte species were sampled in 40 m × 40 m (0.16 ha) plots in primary forest, jungle rubber gardens and rubber plantations throughout the peneplain of Jambi province, Sumatra (Beukema and Van Noordwijk 2004; H. Beukema, unpublished data). Total sampled area for terrestrial pteridophytes was 1.76 ha in 11 primary forest plots, 3.68 ha in 23 jungle rubber plots (in 23 different gardens) and 2.72 ha in 17 rubber plantation plots (in 17 different plantations). Epiphytic pteridophytes were sampled in the same plots except for one primary forest plot that was not sampled for epiphytic pteridophytes. The epiphytic species *Asplenium nidus* L. and *A. phyllitidis* Don were analysed as one species because of difficulty of identification. Age ranges of the rubber plots were characteristic of the productive phase of the respective land use types: 9–74 years old for jungle rubber plots, and 5–19 years old for rubber plantation plots. Of the jungle rubber plots, 57% were in older gardens (>30 years old). The size of sampled primary forest fragments ranged from a few ha to 900 ha. Mean garden size of sampled jungle rubber gardens was 2.2 ha. Of the 17 rubber plantation plots, 11 were in smallholder plantations with an average size of 2.4 ha, while 6 plots were in large plantations covering tens to hundreds of hectares. Sampling took place in 1996, 1997 and 1998.

SUBGROUPS OF VASCULAR PLANTS

In the pteridophyte plots described above, presence/absence of palms (including rattans), lianas, and epiphytic orchids was noted. A subgroup was present in a plot when at least one individual of any size belonging to that subgroup was found in the plot, regardless of species.

TREES

An overview of datasets on trees collected by different researchers in either forest or jungle rubber is given in Table 5.1. For trees, we found no single dataset from Sumatra that included both forest and jungle rubber samples. However, several datasets collected by different researchers in either forest or jungle rubber could be compared as they all distinguished individuals at the species level, used area-based plots and measured tree size as Diameter at Breast Height (DBH). Trees with a minimum size of 10 cm DBH were selected from the datasets in Table 5.1 to be included in our analysis. Laumonier (1997) collected the data used in this study in 1991–1992. Franken and Roos (1981) sampled in 1981. The jungle rubber plot by Vincent *et al.* (unpublished data, ICRAF 2001) was 34 years old when sampled in 1999. Ages of the 16 jungle rubber gardens sampled in 1998–1999 by Hardiwinoto (1999) are unknown. The jungle rubber plot by De Foresta (1991) was about 35 years old when sampled in 1991, while the four plots by Kheowvongsri (1990) were 10, 15, 15, and over 20 years old when sampled in 1990.

BIRDS

We used bird studies over a range of land uses by Danielsen and Heegaard (1995, 2000) and Thiollay (1995), and a rapid assessment by Jepson and Djarwadi (1999), see Table 5.2. Danielsen and Heegaard used a variable distance line-transect method (Buckland *et al.* 1993), while Jepson and Djarwadi collected their data by roaming around a plot centre during three hours by two persons. Thiollay did not sample for a fixed period of time, but finished a sample when 50 individuals were recorded. A list of observations from all three datasets is presented in Appendix 5.2. Further details on the field methods are provided in Danielsen and Heegaard (1995, 2000), Jepson and Djarwadi (1999), and Thiollay (1995).

Table 5.1 Tree datasets. Type and size of sampling unit, sample size, and total area sampled for tree diversity data of several authors. Data from Jambi province, except for De Foresta's jungle rubber plot in South Sumatra. The plot by Vincent (permanent sampling plot, G. Vincent *et al.*, unpublished data, ICRAF 2001) is in one of the gardens sampled by Hardiwinoto.

Author	Sampling unit	Land use type	Number of sampling units (plots or subplots)	Sampled area
Laumonier	0.04 ha subplots	Primary forest	150 contiguous subplots	6 ha
Franken and Roos	0.2 ha plots	Primary forest	3 plots, different locations	0.6 ha
Vincent *et al.*	0.04 ha subplots	Jungle rubber	25 contiguous subplots in one garden	1 ha
Hardiwinoto *et al.*	0.2 ha plots	Jungle rubber	16 plots in 16 different gardens in 4 villages	3.2 ha
De Foresta	0.1 ha plot	Jungle rubber	1 plot (in 1 garden)	0.1 ha
Kheowvongsri	Various plot sizes	Jungle rubber	4 plots in different gardens (0.05 + 0.07 + 0.12 + 0.13 ha)	0.37 ha

Table 5.2 Bird datasets. Sampling method, sampling effort, and number of bird individuals recorded for bird diversity data of several authors. Data from Jambi (Jepson and Djarwadi, Thiollay) and Riau (Danielsen and Heegaard).

Author and sampling method	Land use type	Sampling effort	Recorded bird individuals
Danielsen & Heegaard; observers moving along a 2,000 m line transect	Primary forest	1 transect; 40 man-hours	1,291
	Jungle rubber	1 transect through several gardens; 40 man-hours	1,281
	Rubber plantation	1 transect through 1 plantation; 20 man-hours	3,014
Jepson & Djarwadi; observers moving within 30 m of a plot centre	Primary forest	2 plots in 1 forest; 12 man-hours total	Not recorded
	Jungle rubber	1 plot (in 1 garden); 6 man-hours	Not recorded
	Rubber plantation	1 plot (in 1 plantation); 6 man-hours	Not recorded
Thiollay; 50 individuals per transect	Jungle rubber	28 transects, >300 m apart, in different gardens in 20 km radius	1,388

How many gardens were covered by the jungle rubber transect of Danielsen and Heegaard (1995, 2000) is unknown, but since the average size of jungle rubber gardens in their study area was 1.2 ha (A. Angelsen, pers. comm.), their 2,000 m transect must have crossed a number of gardens. Although ages of those gardens are unknown, data on tree height and composition suggest that some older gardens were included in their study. Of 81 trees (>10 cm DBH) measured along their jungle rubber transect, 36% were rubber trees ranging in height from 9 m to 23 m, while the other trees ranged in height from 6 m to 26 m (Danielsen and Heegaard, unpublished data). The jungle rubber garden (age uncertain) and the rubber plantation (16 years old) sampled by Jepson and Djarwadi (1999) were the same as those sampled by Gillison *et al.* (1999) for vascular plants. The 28 jungle rubber transects in the study by Thiollay must have included many different gardens, but ages are unknown. Thiollay (1995) mentions a range of 30–80% rubber trees, and canopy height of 20–30 m, which suggests that some older gardens were included. Sampling by Danielsen and Heegaard took place in 1991, by Jepson and Djarwadi in 1997 and by Thiollay in 1991 and 1992.

Aerial insectivorous birds were not included in the study as they are almost impossible to detect in closed-canopy forest. Unidentified birds and birds identified to family or genus level but not to species level were excluded from our analyses. Excluded individuals comprised 14.5% of total bird individuals recorded by Danielsen and Heegaard (1995, 2000) and 2.6% of bird individuals recorded in jungle rubber by Thiollay (1995). From the dataset of Jepson and Djarwadi (1999) 10 unidentified species were excluded, all in primary forest.

5.2.3 Species-accumulation curves

To account for effects of scale and sample size, we summarised data where possible as species-accumulation curves. Species-accumulation curves were compiled for terrestrial pteridophytes, epiphytic pteridophytes, trees, and birds in several land use types. For trees, land use types included primary forest and jungle rubber, while for pteridophytes and birds also rubber plantations were included. Curves were generated for each source dataset separately.

To remove the effect of plot order in the accumulation curves, the program EstimateS (Colwell 1997) was used to randomise plot sequence in each sample and derive average values for the cumulative number of species at each number of sampling units. Those derived values for the cumulative number of species were then plotted against the natural logarithm of area (in hectares) or time (in man-hours). Where data for different land use types were collected in a comparable manner, regression lines were drawn through the datapoints for those land use types to facilitate visual comparison. The ranges of area or time over which such linear relationships are shown were determined by the land use type with the smallest number of sampling units. The linear relationships were in fact linear parts of sigmoid relationships, but datasets were not sufficiently large in all cases to show sigmoid relations.

For trees, data from two small datasets (De Foresta 1991, 0.1 ha, and Kheowvongsri 1990, 0.37 ha) were added as single data points to the figure containing the species-accumulation curves.

In addition to the species-accumulation curves for trees that were based on sampled area, we constructed species-accumulation curves for trees based on recorded individuals using the largest datasets collected in primary forest (Laumonier 1997) and in jungle rubber (Hardiwinoto *et al.* 1999). We removed the rubber trees from the jungle rubber data to show diversity of non-rubber trees in jungle rubber gardens as compared to tree diversity in primary forest. Note that the datasets in this comparison were not collected by the same method (contiguous subplots in primary forest versus non-contiguous plots in jungle rubber).

For birds, we compared the datapoints of the smaller dataset of Jepson and Djarwadi (1999) to datapoints belonging to the species-accumulation curves based on the larger dataset of Danielsen and Heegaard (1995, 2000). These two datasets could be compared because sampling effort was quantified by the same measure (man-hours). Species-accumulation curves for terrestrial pteridophytes were published earlier (Beukema and Van Noordwijk 2004).

5.2.4 Species grouping

Individual species of terrestrial pteridophytes and birds were grouped according to their ecological requirements and preferred habitats. Species accumulation curves were subsequently constructed for the subsets of species that were mainly associated with primary and late secondary forest ('forest species').

Terrestrial pteridophytes

Beukema and Van Noordwijk (2004) grouped terrestrial pteridophytes ecologically according to preferred light conditions and habitat as documented in the literature. Species classified as 'forest species' were all species that require shade or deep shade plus species that prefer light shade and grow in forest. Classified as 'non-forest species' were all species of open and open/light shade conditions plus species that prefer light shade and habitats other than forest (roadsides, forest edges, plantations etc.). For a list of species names and their classification see Beukema and Van Noordwijk (2004).

Birds

Bird species were grouped by preferred habitat (see Appendix 5.2) using data in Van Marle and Voous (1988) and MacKinnon and Phillipps (1993), supplemented with Winkler *et al.* (1995) and personal observations by Danielsen and Heegaard in Sumatra. We classified bird species broadly into three categories (modified from Thiollay 1995) according to their main natural habitat in lowlands and their level of association with lowland forest, as follows:

Habitat group 1 = Species mostly associated with the primary and old secondary forest interior. Some of them are restricted to large, undisturbed forest tracts, but others are more tolerant of human or natural disturbance and remain widespread in more secondary forests.

Habitat group 2 = Species mostly found along edges, in gaps (tree falls, landslides), or in the upper canopy of dense forest stands or in semideciduous, more open forest types. They readily occupy degraded secondary forests, tree plantations, and clearings.

Habitat group 3 = Species of open woodlands, low secondary growth, grasslands, inhabited and cultivated areas.

To analyse changes in bird species composition with disturbance, we compared the relative importance of habitat groups in the three land use types. This was done by calculating, for each dataset, the relative number of species of each habitat group in each land use type expressed as a percentage of the total number of species recorded for that land use type.

5.2.5 Relative species richness

To summarise our data on species diversity in jungle rubber as compared to that in primary forest, and to compare subgroups with each other for the effect of disturbance on their relative species richness, we expressed for each subgroup the species richness in jungle rubber as a percentage of the species richness in undisturbed forest, by sampled area for plant groups and by sampling time for birds. Percentages for terrestrial and epiphytic pteridophytes, trees, and birds were based on the average cumulative richness values derived after randomising plot sequence in EstimateS. For trees, percentages were calculated by comparing datasets that were collected in the same way (either contiguous subplots or plots from different locations in Jambi province).

5.3 Results

5.3.1 Results by group

ALL VASCULAR PLANTS

The datasets by Gillison *et al.* and by De Foresta (see Table 5.1) consisted of a few small plots or transect lines, for which results are displayed in the form of datapoints (Figure 5.2). Both the line transect data and the combined plot data show a decline in species richness with disturbance. Differences in species richness between land use types were larger for the line transect dataset of De Foresta.

SUBGROUPS OF VASCULAR PLANTS

Based on the pteridophyte plots of Beukema, Figure 5.3 shows the percentage of plots in each land use type in which a subgroup was present. This figure shows differences in recolonisation of jungle rubber and rubber plantations by different subgroups of vascular plants. Terrestrial pteridophytes were present in all plots, and we observed that they grew more abundantly in rubber plots than in forest. On the other hand, epiphytic orchids recolonised to a lesser extent than the other subgroups. They were absent from half of the jungle rubber plots and were not found in any of the rubber plantation plots. We observed that epiphytic orchids, when found in jungle rubber, were often represented by only a few immature plants and were always much less abundant than epiphytic pteridophytes. In forest, both epiphytic pteridophytes and epiphytic orchids were abundant and often formed large clumps.

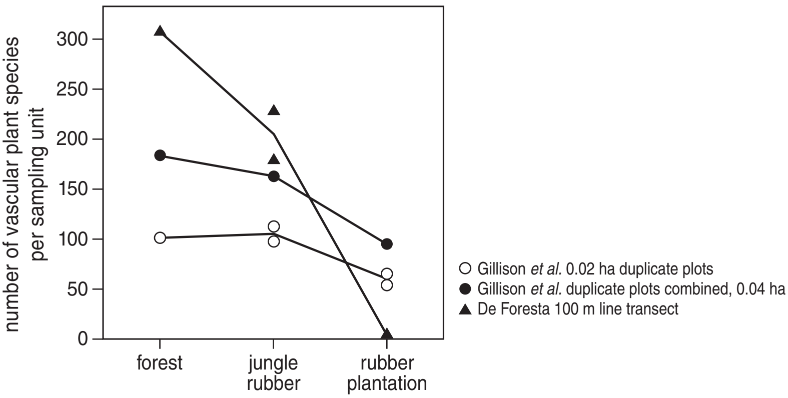


Figure 5.2 Number of species of vascular plants per 100 m line transect (De Foresta) or plot (Gillison *et al.*) in three land use types. De Foresta sampled two different jungle rubber gardens. Gillison *et al.* sampled two 0.02 ha replicate plots per land use type. Replicate plots were located in the same patch of forest, jungle rubber garden or rubber plantation. Datapoints are shown for replicate plots separately (2 points per land use type) and for the combined replicates (one point per land use type representing 0.04 ha).

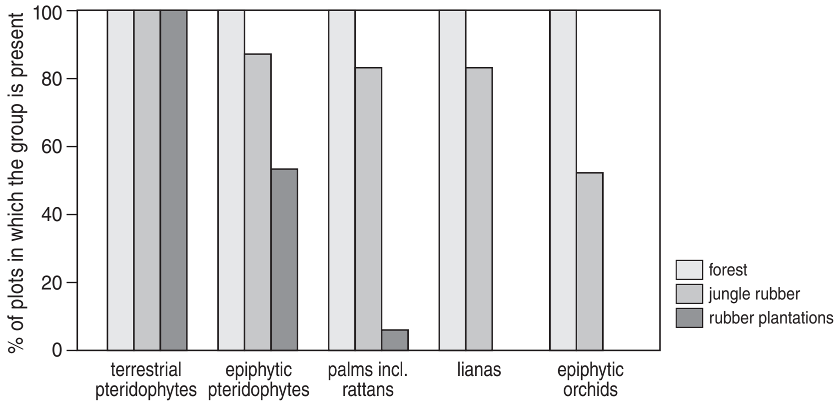


Figure 5.3 Percentage of plots in which a subgroup of vascular plants is represented by at least one individual (11 forest plots, 23 jungle rubber plots and 17 rubber plantation plots of 40 m × 40 m). Lianas and epiphytic orchids are absent from all rubber plantation plots.

With respect to the rubber land use types, Figure 5.3 shows that for all subgroups except terrestrial pteridophytes, presence of subgroups of vascular plants was higher in jungle rubber than in rubber plantations. Palms (including rattans) were found in a single rubber plantation only, while lianas were not found in rubber plantations.

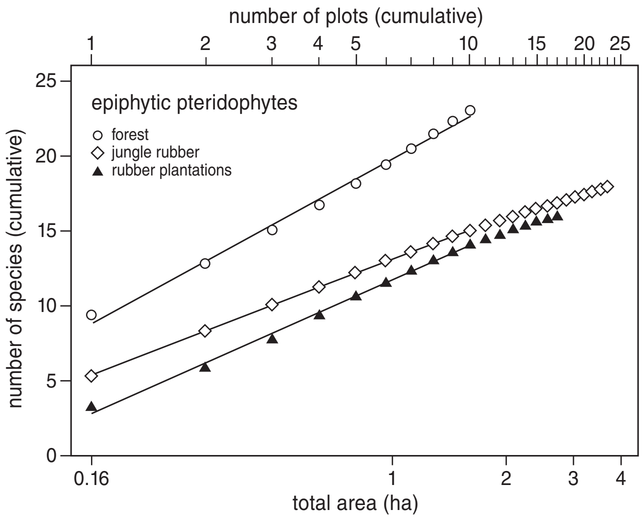


Figure 5.4 Species-accumulation curves for epiphytic pteridophytes in 40 m × 40 m plots in forest (10 plots), jungle rubber (23 plots) and rubber plantations (17 plots) in Jambi province, Sumatra. Data by H. Beukema.

Epiphytic pteridophytes

Species-accumulation curves for epiphytic pteridophytes are shown in Figure 5.4. This figure shows that richness in epiphytic pteridophyte species was lower in jungle rubber than in forest, and somewhat lower again in rubber plantations. The datapoints for rubber plantations were all below those for jungle rubber, and the trend in the data indicates that it is improbable that the curves of jungle rubber and rubber plantations would cross when a larger area would be sampled. However, more samples would be needed to determine whether diversity of epiphytic pteridophytes in rubber plantations is actually similar or slightly lower than in jungle rubber.

A list of scientific names of epiphytic pteridophyte species by land use type is given in Appendix 5.1. With regard to species composition, we noted that most species found in jungle rubber (78%) and rubber plantations (75%) were also found in forest plots. Although these percentages are of course scale-dependent, they serve to indicate that for epiphytic pteridophytes there was apparently not a large shift in species composition. There was a substantial drop in number of species with disturbance however, and 33% of the species found in primary forest plots were never seen in jungle rubber or rubber plantations in the area.

Trees

Species-accumulation curves and individual datapoints from the datasets presented in Table 5.1 are plotted by area in Figure 5.5. This figure shows that tree species richness in jungle rubber gardens was relatively low as compared to primary forest. The figure also shows that tree species richness values for jungle rubber, as collected by different

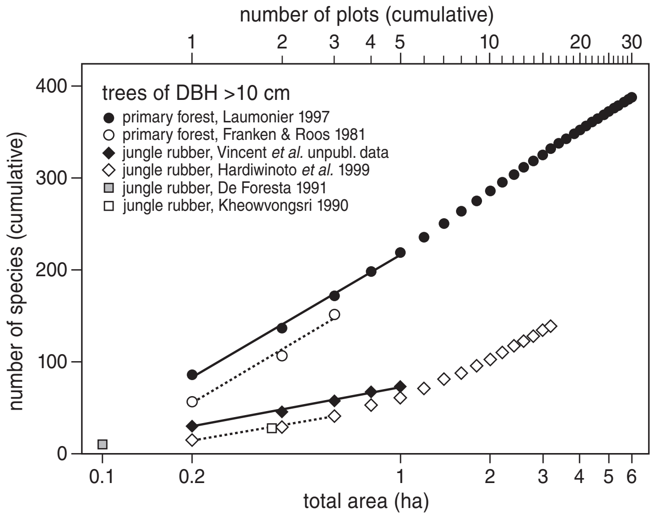


Figure 5.5 Species-accumulation curves and datapoints for trees of DBH over 10 cm, Jambi province, Sumatra. Data by several authors. The plots are contiguous for the dataset by Laumonier (1997, Pasir Mayang) and for the subplots of the 1 ha jungle rubber permanent plot of Vincent (G. Vincent, unpublished data), all other plots are non-contiguous. Regression lines are added for datasets that were collected by the same method: solid lines for contiguous subplots (1 ha), dotted lines for non-contiguous plots (0.6 ha). Four small plots by Kheowvongsri (1990) were lumped together to produce one datapoint. The 0.1 ha plot by De Foresta (1991) is from South Sumatra. For further information about the datasets see the original publications.

researchers, were in close agreement when all results were arranged by sampled area. Of the two forest datasets, richness values found by Franken and Roos (1981) were slightly lower than values found by Laumonier (1997), because one of their three plots was dominated by ironwood (*Eusideroxylon zwageri*) and less rich in other tree species.

Trees excluding rubber

Tree species richness on a per-area basis in rubber agroforests is lowered by the dominance of *Hevea brasiliensis* itself, which is an exotic tree species from South America. With respect to tree species richness, rubber agroforests may probably be regarded as a 'diluted' secondary forest. To have an impression of the size of this 'dilution effect', we have plotted tree species richness of two datasets from Figure 5.5 (Laumonier 1997 for primary forest, Hardiwinoto *et al.* 1999 for rubber agroforests) against the number of individuals sampled, with and without rubber trees (Figure 5.6). It should be noted that data from the two land use types were not collected by the same method: the primary forest data consisted of contiguous subplots in one large forest plot, whereas the rubber agroforest plots were each in a different garden, in several locations.

However large the difference between the data for jungle rubber with and without rubber trees, tree species diversity on a per individual basis was still much higher in primary forest than in jungle rubber. Figure 5.6 also shows a difference between forest and jungle rubber in density of larger trees (DBH over 10 cm).

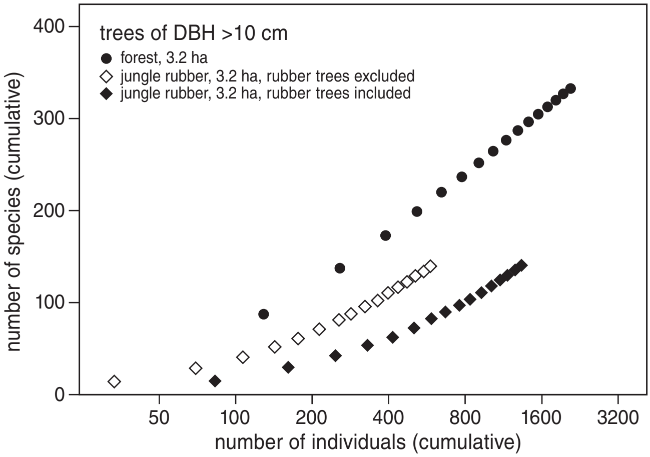


Figure 5.6 Species-accumulation curves for individual trees of DBH over 10 cm, for 3.2 ha of primary forest (Laumonier 1997, dots) and 3.2 ha of jungle rubber (Hardiwinoto *et al*. 1999, diamonds). Filled diamonds: all trees including rubber trees. Open diamonds: rubber trees excluded from the jungle rubber data.

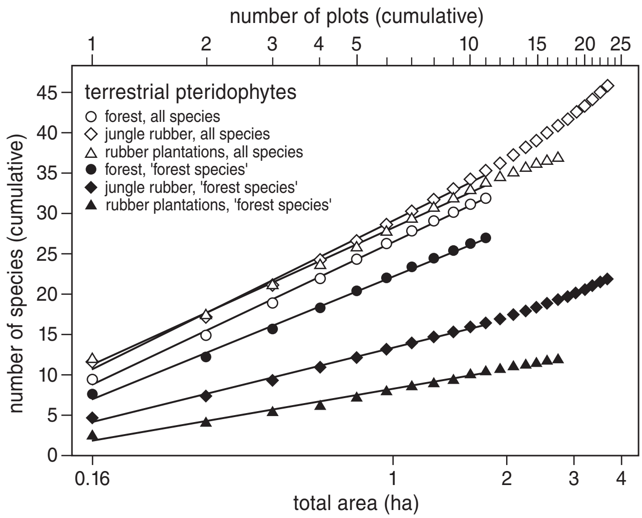


Figure 5.7 Species-accumulation curves for terrestrial pteridophytes in forest (dots), jungle rubber (diamonds) and rubber plantations (triangles). Open symbols: all terrestrial pteridophyte species; filled symbols: 'forest species' subset. Plots were 0.16 ha each, non-adjacent and spread over a large area in Jambi province (see Figure 5.1).

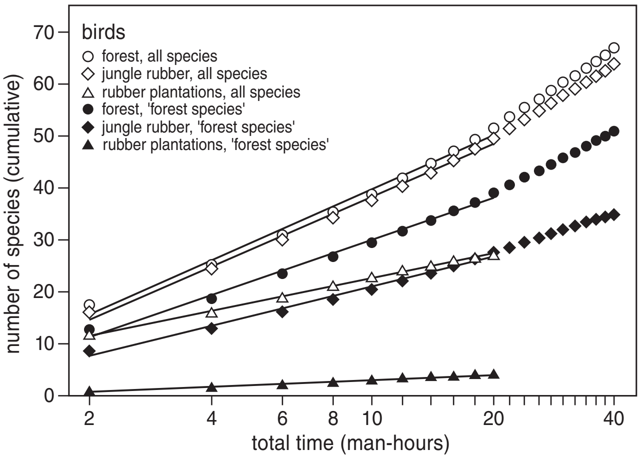


Figure 5.8 Species-accumulation curves for the bird data of Danielsen & Heegaard. Open symbols: all birds identified to species level. Filled symbols: subset of 'forest species' classified in habitat group 1: species mostly associated with the primary and old secondary forest interior.

TERRESTRIAL PTERIDOPHYTES

Species-accumulation curves for all terrestrial pteridophyte species in our dataset and for the 'forest species' subset are shown in Figure 5.7. The 'all species' curves for terrestrial pteridophytes in this figure indicate that species richness was higher in jungle rubber than in both forest and rubber plantations, with forest having the lowest species richness. However, all differences were small in absolute terms, and Figure 5.7 seems to show a flattening trend in the rubber plantations data at larger areas for which we did not have data from forest. The curves for 'forest species' show larger differences in species richness. Forest had the highest richness of 'forest species', followed by jungle rubber, and rubber plantations, which had the lowest richness of 'forest species'. For further details on the terrestrial pteridophyte data see Beukema and Van Noordwijk (2004).

BIRDS: SPECIES-ACCUMULATION CURVES

Figure 5.8 shows species-accumulation curves based on the dataset of Danielsen and Heegaard (1995, 2000) for all birds, and for the subset of 'forest interior birds' of habitat group 1. In this figure, the 'all species' curves for primary forest and jungle rubber are close together, with only slightly higher species richness values for forest. The 'forest species' curves on the other hand show higher species richness in forest than in jungle rubber with respect to bird species that generally prefer the forest interior. Rubber plantations had much lower bird diversity than primary forest and jungle rubber, both for 'all species' and for the 'forest species' subset.

Bird species richness found in the rapid survey by Jepson and Djarwadi (1999) in the three land use types was similar to that found by Danielsen and Heegaard (Figure 5.8) when all species were included. At a sampling effort of 6 man-hours, Jepson and Djarwadi found 30, 33 and 20 species in forest, jungle rubber and rubber plantation respectively, where the average numbers of species in Figure 5.8 at 6 man-hours were 31, 30 and 19, respectively. At a sampling effort of 12 man-hours, Jepson and Djarwadi found 42 species in forest, where in Figure 5.8 the average number of species in forest was also 42. For 'forest species', the trends shown by the two datasets were the same: highest species richness in forest, lowest in rubber plantations, and intermediate values in jungle rubber. The actual numbers of 'forest species' found were not as similar: Jepson and Djarwadi found 19, 14 and 7 species in forest, jungle rubber and rubber plantation respectively at 6 man-hours, versus an average of 23, 16 and 2 species in Figure 5.8. At 12 man-hours, Jepson and Djarwadi found 26 species in forest, versus an average of 32 species in Figure 5.8. Bird data by Thiollay (1995) could not be related to sampling effort in man-hours, so we could not compare this data to our species-accumulation curves.

With regard to bird species composition in primary forest and jungle rubber, the data by Danielsen and Heegaard (Appendix 5.2) show that about half of the species in both primary forest and jungle rubber were also found in the other land use type. A total of 35 species (of which 80% were 'forest species') were found uniquely in primary forest, 32 species (of which 63% were 'non-forest species') were found uniquely in jungle rubber, while 32 species (of which 72% were 'forest species') were found both in primary forest and in jungle rubber.

Birds: habitat preference

We used the grouping of bird species by preferred habitat to compare all three datasets with respect to relative importance (in terms of relative number of species) of the three habitat groups in the three land use types, see Figure 5.9. Results for the different datasets were close together for primary forest and for jungle rubber (maximum 15% difference between datasets), and followed the same, expected pattern of a decrease in 'forest birds' and an increase in birds of more open landscapes from forest to jungle rubber. The dataset of Danielsen and Heegaard showed a continuation of this trend in rubber plantation, as expected. The rubber plantation sample of Jepson and Djarwadi on the other hand contained relatively many 'forest birds' and relatively few birds of habitat group 2 (birds of edges/gaps/plantations).

5.3.2 Relative species richness in jungle rubber

In Figure 5.10 we summarised results of Figures 5.2, 5.4, 5.5, 5.7 and 5.8 by plotting species richness in jungle rubber as a percentage of species richness in primary forest, by area for plants and by sampling time for birds. Figure 5.10 shows that percentages found for relative species richness of terrestrial pteridophytes, birds and epiphytic pteridophytes in jungle rubber, as compared to primary forest, were far apart and that there was no similarity in species richness patterns for these groups. However if we consider the subset of 'forest species' of terrestrial pteridophytes and birds, and we take into account that epiphytic pteridophytes are largely 'forest species' by nature, we find for relative species richness of those 'forest species' in jungle rubber as compared to primary forest a common

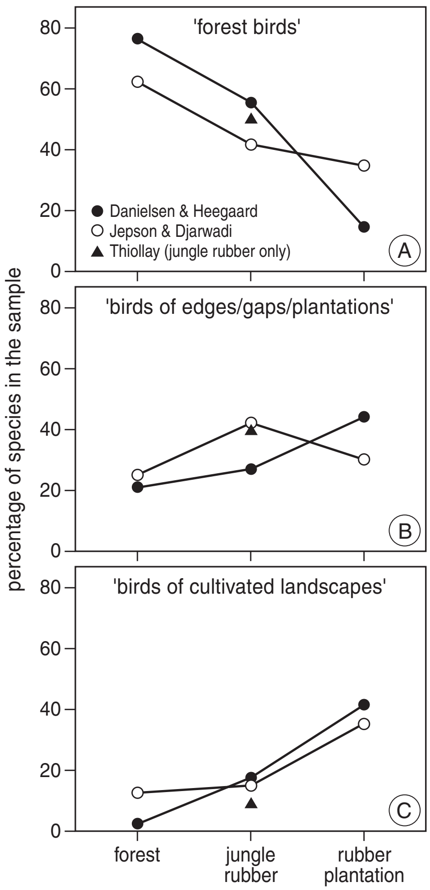


Figure 5.9 Number of bird species belonging to habitat groups (roughly with habitat group 1 = forest birds, 2 = birds of edges/gaps/plantations, and 3 = birds of cultivated landscapes, see Methods section), as a percentage of the total number of bird species found in the land use type, for each dataset separately. Within each land use type, addition of percentages across graphs A, B & C will yield 100% for each dataset.

range of 60–70%. Relative species richness of trees was much lower, around 30%. A reliable percentage for vascular plants as a whole could not be established because available data were all in the range where scale effects are still influential.

In Figure 5.10, scale effects appear only in the first few points of the pteridophyte and bird data series, followed by rather stable percentage values for relative species richness in jungle rubber as compared to primary forest. Note that from this graph we cannot derive the minimal sample size that would have been sufficient to arrive at a stable estimate of the relative species richness percentage, because for each point in Figure 5.10 we used information from our full dataset, whereas smaller datasets would not necessarily show levelling off of the percentages at the same point as in our graph.

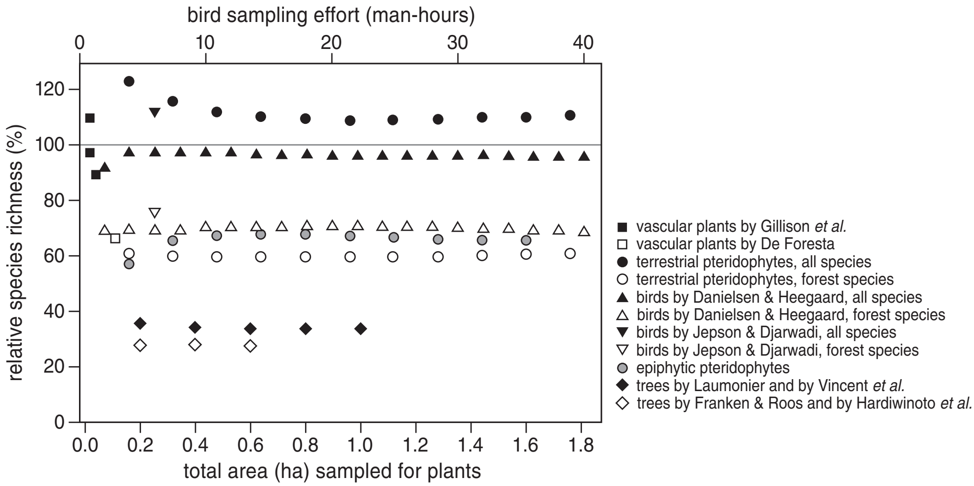


Figure 5.10 Species richness in jungle rubber as a percentage of species richness in primary forest for all vascular plants, for terrestrial and epiphytic pteridophytes, for trees, and for birds. Scale for plants in hectares (lower axis), scale for birds in man-hours (upper axis). Data from Figs 5.2, 5.4, 5.5, 5.7 & 5.8. The duplicates by Gillison *et al.* are displayed both separately (0.02 ha) and combined (0.04 ha). The percentage for De Foresta's dataset is based on the average of two transect lines in jungle rubber compared to one line in primary forest, and is placed at an estimated sampled area of 0.1 ha.

5.4 Discussion and conclusions

5.4.1 Sampling effects

SAMPLE SIZE AND LOCATION

Sampling in one or two jungle rubber gardens only is not likely to give a result that is representative of the jungle rubber land use type as a whole, because of the mosaic character of jungle rubber and the occurrence of scale effects. Also the location(s) of the sample relative to other land uses may have a large influence on the results.

For vascular plants, Figure 5.2 indicates a sampling scale effect similar to that found by Hamer and Hill (2000) for Lepidoptera. In the 0.02 ha plots, no negative effect of disturbance on species richness is found for conversion of forest to jungle rubber, whereas a trend of declining species richness seems to become apparent when species data from the duplicate plots are combined to show results for 0.04 ha. The larger sample by De Foresta shows an even stronger negative effect of disturbance on species richness of vascular plants.

The difference between the two datasets for vascular plants in results for the rubber plantations is most probably due to the choice of plot location. The rubber plantation sampled by Gillison *et al.* (1999) was owned by a private farmer (interviewed by H. Beukema) who stopped yearly fertiliser application 8 years before the sampling took place, and who used herbicides only once, 13 years before sampling. This rubber plantation plot was part of a relatively small section of rubber plantations in a largely forested area. De Foresta sampled a rubber plantation at Sembawa Research Centre (South Sumatra province) where fertilisers and herbicides were applied more intensively, and where the surroundings consisted mostly of cultivated lands.

Jepson and Djarwadi sampled the same rubber plantation as Gillison *et al.* for their bird study, and we suspect that the overrepresentation of 'forest birds' in their rubber plantation data (Figure 5.9A) was an effect of the sampling location being close to forest. Keeping in mind that they sampled for a relatively short time in a single rubber plantation, the choice of location can have this large an effect on the results.

For birds, conclusions from our species-accumulation curves (Figure 5.8) were not in agreement with the rarefaction curves of Thiollay (1995) for forest and jungle rubber. Thiollay found a much higher overall species richness in forest than in jungle rubber whereas we found almost no difference between our 'all species' curves for forest and jungle rubber. Thiollay (1995) mentioned a possible bias caused by differences in altitude and topography, and we suspect that indeed the forest samples were not really comparable to the jungle rubber samples in this case. The forest samples in Thiollay's study were a mixture of lowland and hill samples from three different locations as far as 685 km apart, whereas the jungle rubber samples were all from a single lowland location. The greater altitudinal and geographical range of the forest samples may have caused the higher species richness in forest as compared to jungle rubber. For this reason we did not include Thiollay's forest samples in our analyses.

SURROUNDING LANDSCAPE MATRIX

Jungle rubber gardens are never far from a river, road or village, usually within a distance of about 5 km, as heavy slabs of coagulated rubber need to be carried out of the gardens towards a river or road for further transportation, and tapping is often daily. This has resulted in a landscape where adjacent gardens of different age and management intensity form broad bands along rivers and roads and around villages, and where jungle rubber areas belonging to different villages are often connected along rivers throughout the landscape. Historically, those jungle rubber areas were embedded in a matrix of lowland rainforest. Logging, forest fragmentation and conversion have since changed that matrix in large areas, especially in the lowlands of the central part of Jambi province. Most of our sampling in jungle rubber took place from 1991 to 1999, when major land use change was ongoing. Depending on the location where the sampling took place, the surrounding matrix either somewhat reflected the historical situation with the nearest forest being a large forest area, although sometimes already (partly) altered by logging, or the new situation in which the matrix had been drastically altered and the nearest forest was a small forest fragment or a somewhat larger area of fragmented and logged forest.

Land use change processes may have affected our results in different ways depending on the sampling location and the sampled group. The three studies on birds were all in areas where the nearest forest was a large forest area. Riau province, where Danielsen and Heegaard sampled, was in the 1990s still much less logged and deforested than Jambi province (F. Stolle, pers. comm.). The primary forest in their sample was within an area of approximately 160,000 ha of primary forests, about 3 km away from the jungle rubber. The jungle rubber in their sample was adjacent to slash-and-burn areas and low secondary growth. Jepson and Djarwadi sampled in a jungle rubber garden in a largely agricultural area with rubber plantations and low secondary vegetation, at about 13 km from a large forest concession area in the north of Jambi province. Their primary forest sample was in a 900 ha primary forest study area within the concession. Thiollay sampled in jungle rubber gardens about 10 km away from the edge of the forested area of the foothills of the Barisan Range. Although the immediate plot surroundings in the bird studies consisted mostly of other jungle rubber gardens, plantations and agricultural land, the large forest areas nearby may have been a source for birds recorded in the jungle rubber. The results of the bird studies may not be as representative of jungle rubber gardens in more deforested areas, where bird species richness and composition may be somewhat different.

For plants, nearby forests can be important as source areas for both plant seeds and populations of pollinators and dispersers. The jungle rubber plots of both De Foresta and Gillison *et al.* were in areas where the nearest forest was a large forest area. De Foresta sampled near the Barisan Range, in the same area as the bird study by Thiollay. One of his jungle rubber transects was located in the middle of a relatively small agroforest area of a few ha, next to a 4–5 km belt of slash-and-burn mosaic with fallows less than 5 years old that bordered the forest. The other jungle rubber transect was in a large rubber agroforest area of hundreds of ha that was connected to the forest. The transect was located at about 1 km from the border of this forest. Gillison *et al.* sampled the same plots as Jepson and Djarwadi, described above. The results of the vascular plant studies by De Foresta and Gillison *et al.* may not be as representative of jungle rubber gardens in more deforested areas, where overall plant species richness and composition may be somewhat different.

For pteridophytes, the influence of the distance to forest and the size of forest fragments may be less important, as pteridophytes do not require pollinators, and spores are wind-dispersed. Results are likely to be representative for jungle rubber in Jambi, as pteridophytes were sampled in a wide range of locations both in the central part of Jambi province and in the more forested areas near the Bukit Tigapuluh range. Distance to primary forest ranged from 2 km to 37 km, and averaged 13 km.

The main datasets for trees in jungle rubber, by Vincent *et al.* and Hardiwinoto *et al.*, were collected in a now largely deforested area in the central and southern part of Jambi province. Distance to small fragments of primary forest ranged from 2 km to 30 km, and averaged 17 km. Some plots may have been closer to a somewhat larger area of fragmented and logged forest than to the small primary forest fragments for which distances were calculated. While sampling locations represented a largely deforested landscape, the dataset probably reflects a past situation in which more forest was present in the area because only trees with a minimum size of 10 cm DBH were selected, creating a time lag.

The future potential of jungle rubber to contribute to the conservation of forest species will largely depend on the extent to which viable populations can be maintained inside jungle rubber areas, and on the availability of forest nearby as a source area for biodiversity in jungle rubber.

Sampling method

For tree data, the largest forest dataset consisted of 6 ha of contiguous subplots within one large forest plot, whereas jungle rubber datasets consisted mostly of plots from different gardens in different locations. Jungle rubber gardens are usually small, varying in size from less than a hectare to a few hectares. The largest jungle rubber dataset that consisted of contiguous subplots was 1 ha in size and was collected in one garden. Although comparable in method to the large forest dataset, this dataset from a single garden may not have represented tree diversity in the mosaic of the jungle rubber land use type as well as the larger (3.2 ha) dataset that was collected in many different gardens.

For birds, there may have been variations in detectability caused by differences in vegetation structure. Some jungle rubber gardens are more managed than others, and have a more open understorey. Some cryptic and understorey bird species may have been easier to detect in those gardens than in primary forest. Most birds were however detected by their vocalisations, so differences in detectability caused by habitat variations is unlikely to be important (see Danielsen and Heegaard 1995 p. 83 where this is further discussed).

5.4.2 Representativeness of groups

When species richness is compared over a range of land uses, different patterns emerge for different groups. In Costa Rica, Harvey *et al.* (2006) found that dung beetle species richness was greatest in forests, intermediate in cocoa agroforestry systems, and lowest in plantain monocultures, while mammal species richness was higher in forests than in either cocoa agroforestry systems or plantain monocultures. In a study in Cameroon, Lawton *et al.* (1998) assessed whether changes in species richness of different groups of organisms (birds, soil nematodes and several arthropod groups) over a disturbance gradient from near primary forest to fallow vegetation were correlated. They found that “on average, only 10–11% of the variation in species richness of one group is predicted by the change in richness of another group” and conclude that “attempts to assess the impacts of tropical forest modification and clearance using changes in the species richness of one or a limited number of indicator taxa to predict changes in richness of other taxa may be highly misleading”. Our results for vascular plants and birds point in the same direction with regard to species richness. Terrestrial pteridophytes were found to be slightly more species rich in jungle rubber than in primary forest, whereas species richness of epiphytic pteridophytes and trees was much lower in jungle rubber than in primary forest. Species richness of vascular plants as a whole was lower in jungle rubber than in primary forest, but this could indeed not be predicted from the relative species richness of one or a limited number of subgroups. For birds we found no real difference in total species richness between jungle rubber and primary forest within the relatively short sampling time. We agree with Lawton *et al.* (1998) that changes in overall species richness of individual taxa or subgroups as such are not informative enough to study impacts of forest conversion. However, our findings suggest that when we take ecological characteristics of species into account, relative species richness of ‘forest species’ may be a useful indicator of the biodiversity conservation value of the jungle rubber land use type (see also Basset *et al.* 1998). As the biodiversity conservation value of jungle rubber tends to be overestimated by including species that are not usually associated with primary forest, we see a clear need for ecological information at the species level to allow for species classifications that are relevant to conservation.

Danielsen and Heegaard (2000) found a reduction of specialised insectivore birds of the mid-canopy and understorey, and of woodpeckers, in jungle rubber as compared to forest; they also found that birds are affected by regular presence of rubber tappers and by hunting, reflected in a reduction of pheasants. Several studies in tropical America and Africa concur with our results: high bird species richness in agroforests as compared to nearby forests, but altered composition with regard to ecological groups. For example, Tejeda-Cruz and Sutherland (2004) found that shade coffee plantations in southern Mexico had bird diversity levels similar to, or higher than, natural forest, but supported mostly generalist species, not forest specialists. Shade cacao plantations in Bahia (Faria *et al.* 2006) were characterized by a loss of understorey specialists and an increase of more open area and generalist bird species as compared to nearby forest fragments. In shade-grown yerba mate in Paraguay, 66% of the 145 bird species that were regularly recorded in nearby forest were also regularly recorded in the plantation, but forest floor and understorey bird species were absent (Cockle *et al.* 2005). In Cameroon, a number of bird groups and guilds were found to be significantly different in species richness in forest, agroforestry systems (cacao, coffee, plantain), and annual cultures (Waltert *et al.* 2005).

5.4.3 Conservation and production in rubber agroforests

The role that rubber agroforests can play in biodiversity conservation is limited by the fact that it is a production system that has to be profitable for the farmer. Management practices such as planting, weeding and selection as well as the length of the planting cycle affect vegetation composition and recolonisation by wild species. Even when rubber gardens are not regularly cleaned, farmers generally support desired tree species, either wild or planted, by protecting seedlings, while unwanted tree species are actively removed from gardens by slashing and ring-barking.

Werner (1999) compared the vegetation of secondary forest, cleaned rubber gardens and unmanaged rubber gardens in Kalimantan, and concluded that “regular selective cleaning practices are the major reason for differences in botanical composition and biodiversity of rubber gardens and unmanaged fallow”. Rubber gardens in her study had lower numbers of tree species than unmanaged secondary forests. She also found that the difference in number of species between secondary forest and rubber gardens was more pronounced for tree species than for other vegetation groups. In Singapore, Turner *et al.* (1997) found that the mean tree species number per plot in a diverse type of approximately 100-year-old secondary forest was about 60% of that in primary forest, which is much higher than the relative tree species richness in jungle rubber found in this study (around 30%).

Length of the planting cycle is a major limitation for biodiversity conservation in jungle rubber. Jungle rubber is replanted when the number of rubber trees and latex production become too low to be profitable, on average after about 40 years. Late-successional trees may not reproduce in such a short time, and plant groups such as epiphytes that depend on later successional stages of forest may not have had enough time to establish and reproduce. We found that several epiphytic pteridophyte species observed in forest were never found in jungle rubber. Those species may be limited to much older secondary forest or to primary forest. Epiphytic orchids are known to colonise secondary forest more slowly than epiphytic pteridophytes (Johansson 1974). We observed that epiphytic orchids were present in fewer jungle rubber plots than epiphytic pteridophytes (Figure 5.3), with lower abundance, and were never found flowering or with seeds in jungle rubber gardens.

Although birds can seek out older and less managed gardens, some habitat characteristics of primary forest are rare or lacking in disturbed forest, resulting in a changed community structure of birds with respect to feeding guilds (Danielsen 1997, McGowan and Gillman 1997).

While we acknowledge that irreparable damage has been done to lowland forests in Sumatra, and that many species are threatened and unlikely to find a suitable habitat in jungle rubber or other disturbed forest types (see also Waltert *et al.* 2004), we do want to emphasize the role that jungle rubber can play in the landscape. The importance of jungle rubber for biodiversity conservation in a largely deforested landscape, increasingly dominated by plantations, cannot be stressed enough. The very low richness values for 'forest species' of plants and birds in rubber plantations and the absence of whole groups of organisms from rubber plantations as shown in this paper are clear indicators of the impoverished landscape that is being created by the current large scale conversion process. Although biodiversity in jungle rubber is much reduced compared to primary forest, it is an invaluable biodiversity refuge especially in areas bordering (logged) forest.

Acknowledgements

We thank Arild Angelsen, Hubert de Foresta, Andy Gillison, Morten Heegaard, Paul Jepson, Yves Laumonier, Nining Liswanti, Marco Roos and Jean-Marc Thiollay for permission to use their data and/or clarifying details of datasets. A species-accumulation curve for tree data of Hardiwinoto *et al.* was previously presented in Joshi *et al.* (2000). We thank Morten Heegaard, Mark van Nieuwstadt, Michael Poulsen, Marinus Werger and several anonymous reviewers for commenting on the manuscript. Thanks to Fred Stolle for cartography of Figure 5.1. and to Dr. P.H. Hovenkamp and Dr. H.P. Nooteboom of the National Herbarium of the Netherlands for checking species identifications of pteridophytes. The research by Beukema, Gillison *et al.*, Hardiwinoto *et al.*, and Jepson and Djarwadi was part of the 'Alternatives to Slash-and-Burn' Programme co-ordinated by the World Agroforestry Centre (ICRAF). The research by H. Beukema was sponsored by the Netherlands Organisation for Scientific Research (NWO), UNESCO and ICRAF. The research of Danielsen was part of the NORINDRA project funded by the Indonesian Institute of Science and NORAD.

References

Andrew P (1992) The birds of Indonesia—a checklist (Peters' Sequence). Indonesian Ornithological Society, Jakarta, Indonesia

Basset Y, Novotny V, Miller SE, Springate ND (1998) Assessing the impact of forest disturbance on tropical invertebrates: some comments. J Appl Ecol 35:461–466

Beukema H, Van Noordwijk M (2004) Terrestrial pteridophytes as indicators of a forest-like environment in rubber production systems in the lowlands of Jambi, Sumatra. Agr Ecosyst Environ 104:63–73

Buckland ST, Anderson DR, Burnham KP, Laake JL (1993) Distance sampling: estimating abundance of biological populations. Chapman and Hall, London, UK

Burger K, Smit HP (1998) Prospects for natural rubber after the crisis in Asia. Economic and Social Institute, Free University, Amsterdam, The Netherlands

Burger K, Smit HP (2000) Natural rubber in the new millennium, policies and projections. Economic and Social Institute, Free University, Amsterdam, The Netherlands

Cockle KL, Leonard ML, Bodrati AA (2005) Presence and abundance of birds in an Atlantic forest reserve and adjacent plantation of shade-grown yerba mate in Paraguay. Biodivers Conserv 14:3265–3288

Collins WW, Qualset CO (eds) (1999) Biodiversity in agroecosystems. CRC Press, Boca Raton, Florida, USA

Colwell RK (1997) EstimateS: Statistical estimation of species richness and shared species from samples. Version 5. http://viceroy.eeb.uconn.edu/estimates. User's Guide and application 1997

Danielsen F (1997) Stable environments and fragile communities: does history determine the resilience of avian rain-forest communities to habitat degradation? Biodivers Conserv 6:423–433

Danielsen F, Heegaard M (1995) Impact of logging and plantation development on species diversity—a case study from Sumatra. In: Sandbukt Ø (ed) Management of tropical forests: towards an integrated perspective. Centre for Development and the Environment, University of Oslo, Norway, pp 73–92

Danielsen F, Heegaard M (2000) The biodiversity value of 'Intermediate Systems' of forest management as an alternative to logged forests and plantations: birds in the traditional agroforests of the Sumatran lowlands. Paper presented at the Workshop on Cultivating (in) tropical forests; The evolution and sustainability of intermediate systems between extractivism and plantations, Lofoten, Norway, 28 June–1 July 2000

De Foresta H (1991) Smallholder rubber plantations viewed through forest ecologist glasses—An example from South Sumatra. Paper dated 1991 presented at the Workshop of the Smallholder rubber agroforestry project (USAID/GAPKINDO/IRRI/CIRAD/ICRAF-Indonesia), Bogor, Indonesia, 29–30 September 1997

Dinas Perkebunan (1998) Statistik perkebunan Jambi tahun 1996–1997. Pemerintah propinsi daerah tk. I Jambi, dinas perkebunan, Jambi, Sumatra, Indonesia

Ekadinata A, Widayati A, Vincent G (2004) Rubber agroforest identification using object-based classification in Bungo District, Jambi, Indonesia. Paper presented at the 25th Asian Conference on Remote Sensing, Chiang Mai, Thailand, 22–26 November 2004.
Available at http://www.definiens.com/documents/publications_earth2004.php

Faria D, Laps RR, Baumgarten J, Cetra M (2006) Bat and bird assemblages from forests and shade cacao plantations in two contrasting landscapes in the Atlantic Forest of southern Bahia, Brazil. Biodivers Conserv 15:587–612

Franken NAP, Roos MC (1981) Studies in lowland equatorial forest in Jambi province, Central Sumatra. BIOTROP, Bogor, Indonesia

García-Fernández C, Casado MA, Pérez MR (2003) Benzoic gardens in North Sumatra, Indonesia: effects of management on tree diversity. Conserv Biol 17:829–836

Garrity DP (2004) Agroforestry and the achievement of the Millenium Development Goals. Agroforest Syst 62:5–17

Gillison AN, Liswanti N, Suhardjono, Afriastini JJ, Purnomo E (1999) Vegetation and land use types.

In: Gillison AN (ed) Draft. Above-ground biodiversity assessment working group summary report 1996–1998. Alternatives to slash and burn project phase II, goal 2: impact on biodiversity of different land uses. CIFOR, Jakarta, Indonesia, pp 21–22 and Annex III Table 3 [NB the final version (2000) of this report does not include the species records.]

Gillison AN (ed) (2000) Alternatives to Slash-and-Burn Above-ground biodiversity assessment working group summary report 1996–1999. Impact of different land uses on biodiversity. ASB Coordination Office, ICRAF, Nairobi, Kenya

Gouyon A, De Foresta H, Levang P (1993) Does 'jungle rubber' deserve its name? An analysis of rubber agroforestry systems in southeast Sumatra. Agroforest Syst 22:181–206

Halladay P, Gilmour DA (eds) (1995) Conserving biodiversity outside protected areas. The role of traditional agro-ecosystems. IUCN Forest Conservation Programme, Andalucía, Spain

Hamer KC, Hill JK (2000) Scale-dependent effects of habitat disturbance on species richness in tropical forests. Conserv Biol 14:1435–1440

Hardiwinoto S, Adriyanti DT, Suwarno HB, Aris D, Wahyudi M, Sambas Sn M (1999) Draft report of the research: stand structure and species composition of rubber agroforests in tropical ecosystems of Jambi, Sumatra. Faculty of Forestry, Gadjah Mada University, Yogyakarta, and ICRAF S.E. Asia, Bogor, Indonesia

Harvey C, Gonzalez J, Somarriba E (2006) Dung beetle and terrestrial mammal diversity in forests, indigenous agroforestry systems and plantain monocultures in Talamanca, Costa Rica. Biodivers Conserv 15:555–585

Hill JK, Hamer KC (2004) Determining impacts of habitat modification on diversity of tropical forest fauna: the importance of spatial scale. J Appl Ecol 41:744–754

Jepson P, Djarwadi (1999) Birds. In: Gillison AN (ed) Draft. Above-ground biodiversity assessment working group summary report 1996–1998. Alternatives to slash and burn project phase II, goal 2: impact on biodiversity of different land uses. CIFOR, Jakarta, Indonesia, pp23–33 and Annex III Table 4 [NB the final version (2000) of this report does not include the species records.]

Johansson D (1974) Ecology of vascular epiphytes in West African rain forest. Acta Phytogeogr Suec 59. Uppsala, Sweden

Joshi L, Van Noordwijk M, Wibawa G, Vincent G, Hardiwinoto S, Sukandi T (2000) Gap replanting—an emerging trend in rejuvenation of jungle rubber agroforests in Jambi, Indonesia. Paper presented at the Workshop on Cultivating (in) tropical forests; The evolution and sustainability of intermediate systems between extractivism and plantations, Lofoten, Norway, 28 June–1 July 2000

Kheowvongsri P (1990) Les jardins à Hévéas des contreforts orientaux de Bukit Barisan, Sumatra, Indonésie. Academie de Montpellier, Université des Sciences et Techniques du Languedoc, Montpellier, France

Kubitzki K (1990) The families and genera of vascular plants. Springer, Berlin Heidelberg New York

Lambert FR, Collar NJ (2002) The future for Sundaic lowland forest birds: long-term effects of commercial logging and fragmentation. Forktail 18:127–146

Laumonier Y (1997) The vegetation and physiography of Sumatra. Geobotany 22. Kluwer, Dordrecht, The Netherlands

Lawton JH, Bignell DE, Bolton B, Bloemers GF, Eggleton P, Hammond PM, Hodda M, Holt RD, Larsen TB, Mawdsley NA, Stork NE, Srivastava DS, Watt AD (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. Nature 391:72–76

Levang P, Yoza BK, Tasman A (1999) In the shadow of rubber. Alternative agricultural development perspectives in Jambi. IRD-Orstom and Departemen Transmigrasi dan PPH, Jakarta, Indonesia

MacKinnon J, Phillipps K (1993) A field guide to the birds of Borneo, Sumatra, Java, and Bali, the Greater Sunda Islands. Oxford University Press, Oxford, UK

McGowan P, Gillman M (1997) Assessment of the conservation status of partridges and pheasants in South East Asia. Biodivers Conserv 6:1321–1337

Michon G, De Foresta H (1992) Complex agroforestry systems and the conservation of biological diversity. Agroforests in Indonesia: the link between two worlds. In: Yap SK, Lee SW (eds) Proceedings of the International Conference on Tropical Biodiversity 'In Harmony with Nature', Kuala Lumpur, Malaysia, 12–16 June 1990. Malayan Nature Society, Kuala Lumpur, Malaysia, pp457–473

Michon G, De Foresta H (1995) The Indonesian agro-forest model. Forest resource management and biodiversity conservation. In: Halladay P, Gilmour DA (eds) Conserving biodiversity outside protected areas. The role of traditional agro-ecosystems. IUCN Forest Conservation Programme, Andalucía, Spain, pp 90–106

Ministry of Forestry and Estate Crops, Department of Estate Crops (1998) Statistics of Estate Crops of Indonesia—Rubber. Ministry of Forestry and Estate Crops, Jakarta, Indonesia

Potter L, Lee J (1998) Tree planting in Indonesia: Trends, impacts and directions. CIFOR Occasional Paper No. 18. Available on http://www.cifor.cgiar.org/

Sandbukt Ø, Wiriadinata H (1994) Rain forest and resource management. Proceedings of the NORINDRA seminar, Jakarta, Indonesia, 25–26 May 1993. Indonesian Institute of Sciences (LIPI), Jakarta, Indonesia

Schroth G, Fonseca G, Harvey CA, Gascon C, Vasconcelos H, Izac A-MN (eds) (2004) Agroforestry and biodiversity conservation in tropical landscapes. Island Press, Washington DC, USA and London, UK

Siebert SF (2002) From shade- to sun-grown perennial crops in Sulawesi, Indonesia: implications for biodiversity conservation and soil fertility. Biodivers Conserv 11:1889–1902

Smit HP, Vogelvang E (1997) Changing interactions on markets for competing commodities: the case of natural and synthetic rubber prices. Serie Research Memoranda no. 1997-23. Faculteit der Economische Wetenschappen en Econometrie, Vrije Universiteit, Amsterdam, The Netherlands

Suyanto S, Tomich TP, Otsuka K (2001) Land tenure and farm management efficiency: The case of smallholder rubber production in customary land areas of Sumatra. Agroforest Syst 52:145–160

Tejeda-Cruz C, Sutherland W (2004) Bird responses to shade coffee production. Animal Conserv 7:169–179

Thiollay J-M (1995) The role of traditional agroforests in the conservation of rain forest bird diversity in Sumatra. Conserv Biol 9:335–353

Tomich TP, Van Noordwijk M, Budidarsono S, Gillison A, Kusumanto T, Murdiyarso D, Stolle F, Fagi AM (1998) Alternatives to Slash-and-Burn in Indonesia. Summary report and synthesis of phase II. ASB-Indonesia Report no. 8, ICRAF S.E. Asia, Bogor, Indonesia

Turner IM, Wong YK, Chew PT, Bin Ibrahim A (1997) Tree species richness in primary and old secondary tropical forest in Singapore. Biodivers Conserv 6:537–543

Van Marle JG, Voous KH (1988) The birds of Sumatra. An annotated check-list. B.O.U. Checklist No. 10, British Ornithologists' Union, Tring, UK

Van Noordwijk M, Tomich TP, Winahyu R, Murdiyarso D, Suyanto, Partoharjono S, Fagi AM (1995) Alternatives to Slash-and-Burn in Indonesia. Summary report of phase I. ASB-Indonesia Report no. 4, ICRAF S.E. Asia, Bogor, Indonesia

Waltert M, Mardiastuti A, Mühlenberg M (2004) Effects of land use on bird species richness in Sulawesi, Indonesia. Conserv Biol 18:1339–1346

Waltert M, Bobo KS, Sainge NM, Fermon H, Mühlenberg M (2005) From forest to farmland: habitat effects on Afrotropical forest bird diversity. Ecol Appl 15:1351–1366

Werner S (1999) The impact of management practices on species richness within productive rubber agroforests of Indonesia. In: Sist P, Sabogal C, Byron Y (eds) Management of secondary and logged-over forests in Indonesia. Selected proceedings of an international workshop, Bogor, Indonesia, 17–19 November 1997. CIFOR, Bogor, Indonesia, pp 33–44

Winkler H, Christie DA, Nurney D (1995) Woodpeckers: a guide to the woodpeckers, piculets and wrynecks of the world. Pica Press, Mountfield, Sussex, UK

World Bank (2001) Indonesia. Environment and natural resource management in a time of transition. World Bank, Washington DC, USA

WRI, IUCN, UNEP (1992) Global biodiversity strategy. Guidelines for action to save, study and use earth's biotic wealth sustainably and equitably. World Resources Institute, Washington DC, USA.

Appendix 5.1 Species of epiphytic pteridophytes found in 0.16 ha plots in primary forest (N = 10), jungle rubber (N = 23) and rubber plantations (N = 17) in the lowlands of Jambi province, Sumatra; data by H. Beukema. Values reflect the percentage of plots in each land use type in which the species was found. Families according to Kubitzki (1990).

Family	**Species**	**Primary forest**	**Jungle rubber**	**Rubber plantations**
Aspleniaceae	*Asplenium nidus* L./*Asplenium phyllitidis* Don	100	70	47
Aspleniaceae	*Asplenium pellucidum* Lam.	0	4	6
Davalliaceae	*Davallia angustata* Wall. ex Hook. & Grev.	10	0	0
Davalliaceae	*Davallia denticulata* (Burm. f.) Mett. ex Kuhn var. *denticulata*	50	43	12
Davalliaceae	*Davallia heterophylla* J. Sm.	20	0	0
Davalliaceae	*Davallia solida* (Forst.) Sw. var. *solida*	90	35	18
Davalliaceae	*Davallia triphylla* Hook.	50	17	0
Dryopteridaceae	*Pleocnemia irregularis* (C. Presl) Holtt.	0	4	0
Lycopodiaceae	*Lycopodium* sp.	10	0	0
Nephrolepidaceae	*Nephrolepis biserrata* (Sw.) Schott	10	30	18
Polypodiaceae	*Drynaria quercifolia* (L.) J.Sm.	50	17	24
Polypodiaceae	*Drynaria sparsisora* (Desv.) Moore	100	87	47
Polypodiaceae	*Goniophlebium percussum* (Cavanilles) Wagner et Grether	20	4	0
Polypodiaceae	*Lecanopteris crustacea* Copel.	20	0	0
Polypodiaceae	*Loxogramme avenia* (Blume) Presl	10	0	0
Polypodiaceae	*Loxogramme* cf. *scolopendrina* (Bory) Presl	10	0	0
Polypodiaceae	*Microsorum membranifolium* (R. Br.) Ching	0	0	6
Polypodiaceae	*Microsorum punctatum* (L.) Copel.	20	26	29
Polypodiaceae	*Microsorum scolopendria* (Burm. f.) Copel.	0	0	12
Polypodiaceae	*Platycerium coronarium* (Koenig) Desv.	10	0	12
Polypodiaceae	*Platycerium ridleyi* Christ.	20	0	0
Polypodiaceae	*Pyrrosia angustata* (Sw.) Ching	90	52	24
Polypodiaceae	*Pyrrosia lanceolata* (L.) Farwell	60	13	24
Polypodiaceae	*Pyrrosia longifolia* (Burm.) Morton	10	0	18
Polypodiaceae	*Pyrrosia piloselloides* (L.) Price	0	17	35
Polypodiaceae	*Selliguea lateritia* (Baker) Hovenkamp	10	0	0
Vittariaceae	*Antrophyum callifolium* Bl.	10	9	0
Vittariaceae	*Vittaria elongata* Sw.	90	65	6
Vittariaceae	*Vittaria ensiformis* Sw.	70	43	0
Vittariaceae	*Vittaria scolopendrina* (Bory) Thwaites	0	4	0
Number of species		24	18	16

Appendix 5.2 List of birds with habitat preference classification, number of individuals in the datasets of Danielsen & Heegaard (D&H) and Thiollay (TH), and presence (1) or absence (0) in the dataset of Jepson & Djarwadi (J&D). Nomenclature follows Andrew (1992).
Habitat class 1 = forest birds, 2 = birds of edges/gaps/plantations, and 3 = birds of cultivated landscapes; see Methods section).

Scientific name	English name	Habitat class	D&H Primary forest	D&H Jungle rubber	D&H Rubber plantation	TH Jungle rubber	J&D Primary forest	J&D Primary forest	J&D Jungle rubber	J&D Rubber plantation
Abroscopus superciliaris	Yellow-bellied Warbler	2	0	0	0	7	0	0	0	0
Accipiter gularis	Japanese Sparrowhawk	3	0	0	0	0	0	0	0	1
Accipiter trivirgatus	Crested Goshawk	1	0	0	0	1	0	0	0	0
Aegithina tiphia	Common Iora	2	0	0	0	10	0	0	0	0
Aegithina viridissima	Green Iora	1	3	0	5	10	0	0	0	0
Aethopyga siparaja	Crimson Sunbird	2	0	1	0	6	0	0	0	0
Alcippe brunneicauda	Brown Fulvetta	1	0	0	0	10	0	0	0	0
Amaurornis phoenicurus	White-breasted Waterhen	3	0	0	6	0	0	0	0	0
Anorrhinus galeritus	Bushy-crested Hornbill	1	0	38	0	5	0	0	0	0
Anthracoceros albirostris	Asian Pied Hornbill	2	0	0	0	0	0	0	1	0
Anthracoceros malayanus	Black Hornbill	2	8	4	0	5	0	0	1	0
Anthreptes malacensis	Brown-throated Sunbird	3	0	0	0	21	1	0	1	0
Anthreptes rhodolaema	Red-throated Sunbird	2	0	0	0	8	0	0	0	0
Anthreptes simplex	Plain Sunbird	1	1	0	0	3	0	0	0	0
Anthreptes singalensis	Ruby-cheeked Sunbird	2	0	0	0	14	0	0	0	0
Aplonis panayensis	Asian Glossy Starling	3	0	0	0	0	1	1	0	0
Arachnothera affinis	Grey-breasted Spiderhunter	1	4	3	0	0	1	1	0	0
Arachnothera chrysogenys	Yellow-eared Spiderhunter	1	0	0	0	4	0	0	0	0
Arachnothera flavigaster	Spectacled Spiderhunter	1	0	0	0	6	0	0	0	0
Arachnothera longirostra	Little Spiderhunter	1	203	127	4	95	1	0	0	0
Arachnothera robusta	Long-billed Spiderhunter	1	0	0	0	1	0	0	0	0
Argusianus argus	Great Argus	1	59	0	0	0	0	0	0	0
Aviceda jerdoni	Jerdon's Baza	1	1	0	0	0	0	0	0	0
Blythipicus rubiginosus	Maroon Woodpecker	1	1	0	0	0	0	0	0	0
Buceros rhinoceros	Rhinoceros Hornbill	1	3	0	0	4	1	0	1	0
Cacomantis merulinus	Plaintive Cuckoo	3	0	16	22	0	0	0	0	0
Cacomantis sonneratii	Banded Bay Cuckoo	2	0	0	0	1	1	0	1	0

Appendix 5.2 Continued

Scientific name	English name	Habitat class	D&H Primary forest	D&H Jungle rubber	D&H Rubber plantation	TH Jungle rubber	J&D Primary forest	J&D Primary forest	J&D Jungle rubber	J&D Rubber plantation
Calorhamphus fuliginosus	Brown Barbet	2	0	4	0	38	0	0	1	0
Calyptomena viridis	Green Broadbill	1	17	0	0	0	0	0	0	0
Celeus brachyurus	Rufous Woodpecker	2	1	1	0	3	0	0	0	0
Centropus bengalensis	Lesser Coucal	3	0	15	0	1	0	0	1	1
Centropus sinensis	Greater Coucal	3	0	15	4	0	0	0	0	0
Cettia vulcania *	Sunda Bush-Warbler	1	0	0	0	0	0	0	1	0
Ceyx erithacus	Oriental Dwarf Kingfisher	1	0	0	0	0	1	1	0	0
Chalcophaps indica	Emerald Dove	1	5	4	0	0	0	0	1	1
Chloropsis cochinchinensis	Blue-winged Leafbird	2	0	0	0	33	0	0	0	0
Chloropsis cyanopogon	Lesser Green Leafbird	2	0	0	4	4	0	0	0	0
Chloropsis sonnerati	Greater Green Leafbird	1	0	0	0	5	1	1	0	0
Chrysococcyx xanthorhynchus	Violet Cuckoo	2	0	0	0	6	0	0	0	0
Copsychus malabaricus	White-rumped Shama	1	17	14	1	28	0	1	0	0
Copsychus saularis	Oriental Magpie-robin	3	0	0	11	9	0	0	0	0
Coracina striata	Bar-bellied Cuckoo-shrike	1	0	0	0	0	1	0	0	0
Corvus enca	Slender-billed Crow	2	9	0	12	3	0	1	1	1
Corvus macrorhynchos	Large-billed Crow	3	0	8	0	0	0	0	0	0
Criniger bres	Grey-cheeked Bulbul	1	0	2	0	6	0	0	0	0
Criniger ochraceus	Ochraceous Bulbul	1	0	0	0	2	0	0	0	0
Criniger phaeocephalus	Yellow-bellied Bulbul	1	1	2	0	6	1	1	0	0
Culicicapa ceylonensis	Grey-headed Flycatcher	1	0	0	0	0	1	0	0	0
Cymbirhynchus macrorhynchos	Black-and-red Broadbill	2	0	0	0	1	0	0	0	0
Cyornis tickelliae *	Tickell's Blue Flycatcher	2	0	0	0	0	1	1	0	0
Cyornis turcosus	Malaysian Blue Flycatcher	1	0	4	0	1	0	0	0	0
Dicaeum cruentatum	Scarlet-backed Flowerpecker	2	0	2	0	20	0	0	0	0
Dicaeum trigonostigma	Orange-bellied Flowerpecker	2	0	0	0	56	1	1	1	0
Dicrurus aeneus	Bronzed Drongo	2	0	0	0	2	0	0	0	0
Dicrurus paradiseus	Greater Racket-tailed Drongo	2	81	37	6	14	1	1	1	0
Dinopium javanense	Common Goldenback	2	0	0	1	0	0	0	0	0

Appendix 5.2 Continued

Scientific name	English name	Habitat class	D&H Primary forest	D&H Jungle rubber	D&H Rubber plantation	TH Jungle rubber	J&D Primary forest	J&D Primary forest	J&D Jungle rubber	J&D Rubber plantation
Dinopium rafflesii	Olive-backed Woodpecker	1	0	0	0	0	1	0	0	0
Dryocopus javensis	White-bellied Woodpecker	1	2	0	0	0	1	1	0	0
Ducula aenea	Green Imperial Pigeon	1	0	0	0	0	0	0	1	0
Eupetes macrocerus	Rail Babbler	1	2	0	0	0	0	1	0	0
Eurylaimus javanicus	Banded Broadbill	1	1	0	0	1	0	0	0	0
Eurylaimus ochromalus	Black-and-yellow Broadbill	2	58	0	8	5	0	0	1	1
Eurystomus orientalis	Common Dollarbird	2	0	0	0	1	0	0	0	0
Gallus gallus	Red Junglefowl	2	0	0	0	1	0	0	0	0
Gracula religiosa	Hill Myna	2	5	34	0	6	0	1	0	1
Halcyon chloris	Collared Kingfisher	3	0	3	0	0	0	0	0	0
Halcyon smyrnensis	White-throated Kingfisher	3	0	0	1	2	0	0	0	1
Harpactes diardii	Diard's Trogon	1	1	0	0	0	0	0	0	0
Harpactes duvaucelii	Scarlet-rumped Trogon	1	0	1	0	2	0	0	0	0
Harpactes kasumba	Red-naped Trogon	1	0	0	0	0	1	1	0	0
Harpactes orrhophaeus	Cinnamon-rumped Trogon	1	1	0	0	0	0	0	0	0
Hemicircus concretus	Grey-and-buff Woodpecker	2	0	2	0	15	0	0	0	0
Hemiprocne comata	Whiskered Tree-swift	2	0	0	0	0	0	1	0	0
Hemipus hirundinaceus	Black-winged Hemipus	2	0	0	11	19	0	1	0	0
Hypogramma hypogrammicum	Purple-naped Sunbird	1	1	5	0	3	0	0	0	0
Hypothymis azurea	Black-naped Monarch	1	2	13	0	20	0	1	1	0
Hypsipetes charlottae	Buff-vented Bulbul	1	0	0	0	3	0	0	0	0
Hypsipetes criniger	Hairy-backed Bulbul	1	8	0	0	19	0	0	0	0
Irena puella	Asian Fairy Bluebird	1	1	3	0	10	0	1	0	0
Kenopia striata	Striped Wren-babbler	1	0	0	0	0	0	1	0	0
Lalage nigra	Pied Triller	3	0	0	2	0	0	0	0	0
Lanius cristatus	Brown Shrike	1	0	1	0	0	0	0	0	0
Lonchura leucogastra	White-bellied Munia	2	0	32	0	0	0	0	0	0
Lonchura striata	White-rumped Munia	3	0	7	296	0	0	0	0	0
Lophura erythrophthalma	Crestless Fireback	1	2	0	0	0	0	0	0	0

Appendix 5.2 Continued

Scientific name	English name	Habitat class	D&H Primary forest	D&H Jungle rubber	D&H Rubber plantation	TH Jungle rubber	J&D Primary forest	J&D Primary forest	J&D Jungle rubber	J&D Rubber plantation
Loriculus galgulus	Blue-crowned Hanging-parrot	2	2	3	0	2	1	1	0	1
Macronous gularis	Striped Tit-babbler	2	47	22	12	8	0	0	1	0
Macronous ptilosus	Fluffy-backed Tit-babbler	1	4	38	0	8	0	0	0	0
Malacopteron affine	Sooty-capped Babbler	1	0	0	0	1	0	0	0	0
Malacopteron cinereum	Scaly-crowned Babbler	1	57	2	0	8	0	1	0	0
Malacopteron magnirostre	Moustached Babbler	1	4	0	0	28	1	1	0	0
Malacopteron magnum	Rufous-crowned Babbler	1	18	0	0	17	1	0	0	0
Megalaima australis	Blue-eared Barbet	2	6	0	0	39	0	0	1	0
Megalaima chrysopogon	Gold-whiskered Barbet	1	48	21	0	0	0	0	0	0
Megalaima haemacephala	Coppersmith Barbet	3	0	0	0	21	0	0	0	0
Megalaima henricii	Yellow-crowned Barbet	1	2	3	0	0	0	0	0	0
Megalaima mystacophanos	Red-throated Barbet	1	0	0	0	10	0	0	0	0
Megalaima rafflesii	Red-crowned Barbet	1	0	0	0	6	1	1	0	0
Meiglyptes tristis	Buff-rumped Woodpecker	2	0	1	8	0	0	0	0	0
Meiglyptes tukki	Buff-necked Woodpecker	1	0	5	0	2	1	0	0	0
Merops viridis	Blue-throated Bee-eater	3	0	0	0	0	0	1	1	1
Microhierax fringillarius	Black-thighed Falconet	2	0	0	0	1	0	0	0	0
Napothera macrodactyla	Large Wren-babbler	1	2	0	0	2	0	0	0	0
Nectarinia jugularis	Olive-backed Sunbird	3	0	0	0	0	0	0	0	1
Nectarinia sperata	Purple-throated Sunbird	2	0	0	0	7	0	0	0	0
Nyctyornis amictus	Red-bearded Bee-eater	1	0	1	0	12	0	0	0	0
Oriolus chinensis	Black-naped Oriole	3	0	1	2	0	0	0	0	0
Oriolus xanthonotus	Dark-throated Oriole	1	46	4	0	1	0	0	1	0
Orthotomus atrogularis	Dark-necked Tailorbird	3	0	0	0	41	0	1	1	1
Orthotomus ruficeps	Ashy Tailorbird	3	0	1	32	29	1	1	0	0
Orthotomus sericeus	Rufous-tailed Tailorbird	2	0	6	0	2	0	1	0	0
Pelargopsis capensis	Stork-billed Kingfisher	3	0	1	0	0	0	0	0	0
Pellorneum capistratum	Black-capped Babbler	1	1	54	0	2	0	0	0	0
Pericrocotus cinnamomeus	Small Minivet	2	0	0	2	0	0	0	0	0

Appendix 5.2 Continued

Scientific name	English name	Habitat class	D&H Primary forest	D&H Jungle rubber	D&H Rubber plantation	TH Jungle rubber	J&D Primary forest	J&D Primary forest	J&D Jungle rubber	J&D Rubber plantation
Pericrocotus flammeus	Scarlet Minivet	1	0	0	0	6	0	0	0	0
Philentoma pyrhopterum	Rufous-winged Philentoma	1	2	0	0	0	0	0	0	0
Philentoma velatum	Maroon-breasted Philentoma	1	8	0	0	0	0	0	0	0
Picus puniceus	Crimson-winged Yellownape	1	0	0	0	1	0	0	1	1
Platylophus galericulatus	Crested Jay	1	3	0	0	0	0	0	0	0
Platysmurus leucopterus	Black Magpie	1	0	0	0	3	0	0	1	1
Pomatorhinus montanus	Chestnut-backed Scimitar-Babbler	1	3	0	0	0	0	0	0	1
Prinia atrogularis *	Hill Prinia	2	0	0	0	2	0	0	0	0
Prinia familiaris	Bar-winged Prinia	3	0	0	1083	0	0	0	1	0
Prinia flaviventris	Yellow-bellied Prinia	3	0	0	0	10	0	0	0	1
Prionochilus maculatus	Yellow-breasted Flowerpecker	1	4	4	0	37	0	0	0	0
Prionochilus percussus	Crimson-breasted Flowerpecker	1	0	3	0	37	0	0	1	1
Psittacula longicauda	Long-tailed Parakeet	2	137	44	300	0	0	0	0	0
Psittinus cyanurus	Blue-rumped Parrot	1	13	2	0	0	1	1	0	1
Ptilinopus jambu	Jambu Fruit-dove	1	0	2	0	0	0	0	0	0
Pycnonotus atriceps	Black-headed Bulbul	2	0	12	0	56	0	0	1	1
Pycnonotus brunneus	Red-eyed Bulbul	1	1	3	0	21	0	0	1	1
Pycnonotus cyaniventris	Grey-bellied Bulbul	1	1	0	0	0	0	0	0	0
Pycnonotus erythropthalmos	Spectacled Bulbul	2	4	0	0	154	0	0	0	0
Pycnonotus eutilotus	Puff-backed Bulbul	1	0	0	0	8	0	0	0	0
Pycnonotus goiavier	Yellow-vented Bulbul	3	0	50	1013	0	0	0	0	0
Pycnonotus melanicterus	Black-crested Bulbul	2	0	11	0	51	0	0	1	1
Pycnonotus melanoleucos	Black-and-white Bulbul	1	8	0	0	0	0	0	0	0
Pycnonotus plumosus	Olive-winged Bulbul	3	1	3	0	14	0	0	0	0
Pycnonotus simplex	Cream-vented Bulbul	1	0	4	0	74	0	0	1	0
Reinwardtipicus validus	Orange-backed Woodpecker	1	1	0	0	2	0	0	0	0
Rhamphococcyx curvirostris	Chestnut-breasted Malkoha	2	0	0	0	5	0	0	0	0

Appendix 5.2 Continued

Scientific name	English name	Habitat class	D&H Primary forest	D&H Jungle rubber	D&H Rubber plantation	TH Jungle rubber	J&D Primary forest	J&D Primary forest	J&D Jungle rubber	J&D Rubber plantation
Rhinomyias olivacea	Fulvous-chested Rhinomyias	1	0	0	0	5	0	0	0	0
Rhinomyias umbratilis	Grey-chested Rhinomyias	1	2	0	0	0	0	0	0	0
Rhinoplax vigil	Helmeted Hornbill	1	26	0	0	0	1	1	0	0
Rhinortha chlorophaea	Raffles's Malkoha	2	0	1	0	2	0	0	0	0
Rhopodytes diardi	Black-bellied Malkoha	2	0	0	0	1	0	0	0	0
Rhopodytes sumatranus	Chestnut-bellied Malkoha	1	0	0	3	0	0	0	1	0
Rhyticeros corrugatus	Wrinkled Hornbill	1	0	2	0	0	0	0	0	0
Rhyticeros undulatus	Wreathed Hornbill	1	0	4	0	0	0	0	0	0
Sasia abnormis	Rufous Piculet	2	1	4	1	2	0	0	1	0
Spilornis cheela	Crested Serpent-eagle	2	7	0	0	1	0	0	0	0
Stachyris erythroptera	Chestnut-winged Babbler	1	42	53	0	14	0	0	1	0
Stachyris maculata	Chestnut-rumped Babbler	1	6	1	0	9	0	0	0	0
Stachyris nigricollis	Black-throated Babbler	1	18	7	0	4	0	0	0	0
Stachyris poliocephala	Grey-headed Babbler	1	2	2	0	12	0	0	0	0
Stachyris rufifrons	Rufous-fronted Babbler	1	0	0	0	4	0	0	0	0
Surniculus lugubris	Drongo Cuckoo	2	0	0	0	1	0	0	1	0
Terpsiphone paradisi	Asian Paradise-flycatcher	1	6	3	0	1	0	1	0	0
Treron olax	Little Green Pigeon	2	3	0	0	0	0	0	0	0
Treron vernans	Pink-necked Green Pigeon	2	0	0	8	5	0	1	0	0
Trichastoma abbotti	Abbott's Babbler	1	0	0	0	0	0	1	0	0
Trichastoma bicolor	Ferruginous Babbler	1	16	0	0	4	0	0	0	0
Trichastoma malaccense	Short-tailed Babbler	1	29	56	0	1	0	0	1	0
Trichastoma pyrrogenys	Temminck's Babbler	1	4	0	0	0	0	0	0	0
Trichastoma sepiarium	Horsfield's Babbler	1	0	0	0	0	1	1	0	0
Zanclostomus javanicus	Red-billed Malkoha	2	1	0	0	2	0	0	0	0

* Record should be considered preliminary until documentation is available.

Chapter 6

The importance of large trees for epiphytic ferns

Hendrien Beukema

Abstract

Rubber production systems may contribute to the conservation of epiphytic ferns in tropical rainforest areas. I investigated the occurrence of fertile and non-fertile epiphytic ferns on different-sized trees in rubber plantations, jungle rubber agroforests and primary forest in the lowlands of Jambi province, Sumatra.

The availability of large trees, the suitability of rubber trees as host trees, and habitat differences caused by land use practices were expected to influence habitat suitability. Length of the slash-and-burn production cycle was on average about 20 years for rubber plantations and 40 years for jungle rubber agroforests. Primary forest and old jungle rubber agroforests (32–74 years) had more large trees than young jungle rubber agroforests (9–26 years) and rubber plantations (5–19 years). In rubber plantations, 98% of trees were rubber trees, whereas on average only 41% of trees in jungle rubber agroforests were rubber trees. Rubber trees were gradually replaced by other trees with increasing age of jungle rubber agroforests.

To assess the importance, by logistic regression, of land use, tree size, and tree type for colonization and reproduction of epiphytic ferns, I recorded the occurrence and fertility status of ferns on rubber trees and other trees in three size classes (Diameter at Breast Height 10–20 cm, 20–40 cm, >40 cm). A total of 3983 trees were checked for epiphytic ferns, of which 949 trees were in primary forest (1.6 ha), 1953 in jungle rubber agroforests (3.68 ha), and 1081 in rubber plantations (2.72 ha).

For the occurrence of epiphytic ferns on trees, only tree size was significant as a main effect. Larger trees were colonized by epiphytic ferns more often than smaller trees. A less important significant interaction indicated that medium sized trees in rubber systems were colonized more often than trees in the same size class in primary forest. For the occurrence of fertile epiphytic ferns on trees, both tree type and tree size were significant as main effects. Rubber trees had fertile epiphytic ferns less often than other trees. Tree size was the most important significant factor, with larger trees having fertile epiphytic ferns more often than smaller trees. Large trees (> 40 cm DBH) had the largest odds ratio (8.27) of any of the factors in the models, indicating an important role for large trees in the reproduction of epiphytic ferns. Primary forest was a significant factor when compared to a reference class of jungle rubber and rubber plantation land use types taken together, indicating that trees in primary forest carried fertile epiphytic ferns more often than trees in the other land use types.

I conclude that rubber plantations contribute little to the conservation of epiphytic ferns, whereas jungle rubber agroforests contribute more as they get older and have more large, non-rubber trees. However, older agroforests also tend to be less productive for the farmer.

6.1 Introduction

6.1.1 Epiphytic ferns of lowland rain forest growing in rubber production systems

Epiphytic ferns growing on trees in jungle rubber agroforests and rubber plantations are a common sight in the Malaysian region. However, the question whether these rubber production systems are contributing substantially to the conservation of epiphytes in tropical lowland rainforest areas has not been studied before. In order to support viable communities of epiphytic ferns, the trees in rubber production systems must not only be suitable for colonization by epiphytic ferns, but those ferns must also produce spores within the limited time of a single slash-and-burn cycle.

In this chapter, I analyse the importance of tree size, tree type (rubber vs. other tree species), land use, and their interactions, for colonization and reproduction by epiphytic ferns in the lowlands of Jambi province in Sumatra.

My research questions were:

- Is the occurrence of epiphytic ferns on trees related to land use, tree size, and is it important whether the tree is a rubber tree or not?
- Is the occurrence of fertile epiphytic ferns on trees related to land use, tree size, and whether the tree is a rubber tree or not?
- How does the epiphyte habitat in jungle rubber and rubber plantations differ from that in primary forest, and how can those differences affect the suitability of these systems for contributing to the conservation of epiphytic ferns?

6.1.2 Jungle rubber agroforests and rubber plantations in Jambi province, Sumatra

Jungle rubber is a species-rich and structurally complex type of agroforest that includes wild species (Beukema *et al.* 2007, Gouyon *et al.* 1993, Werner 1999), whereas rubber plantations are usually monocultures, or include few other planted tree species. Both jungle rubber agroforests and rubber plantations are planted after slash-and-burn land clearing. Rubber plantations are highly managed, including the use of herbicides and fertilisers, and are structurally simple with a single tree layer and a low herb layer underneath. In Jambi, tapping usually starts after 5–6 years and continues until the plantation is about 20 years old.

Jungle rubber is a type of rubber agroforest in which rubber is planted together with rice, vegetables, herbs, and a limited number of useful trees such as fruit trees. No herbicides or fertilisers are used. Weeds are controlled manually for the first 2 or 3 years when rice and vegetables are produced. Management in subsequent years is minimal, and spontaneous secondary vegetation is mostly tolerated. The resulting vegetation resembles a secondary forest dominated by rubber trees. Trees other than rubber are mostly natural regrowth, while some other trees are planted by the farmer. Tapping in jungle rubber usually starts around 9 years after planting. Through natural regeneration of rubber seedlings and active replanting in gaps by the farmer, jungle rubber agroforests can remain productive much longer than rubber plantations. The age at which a jungle rubber agroforest is replanted is on average about 40 years but varies greatly, and some agroforests can get very old, up to a maximum of about 80 years in Jambi province.

6.1.3 Epiphyte presence on small and large trees

Because of a slash-and-burn cultivation cycle in the study area of around 20 years for rubber plantations, and around 40 years for jungle rubber, those systems do not have as many large trees as primary forest. This scarcity of large trees may be an important factor limiting the development of viable populations of epiphytic fern species. Indeed, larger trees are colonized by epiphytes more often than smaller trees, and tend to carry larger epiphyte loads and a more diverse epiphyte flora than smaller trees (Johansson 1974, Benzing 1990, Dunn 2000, Hietz 2005, Wolf 2005, Benavides *et al.* 2006, Flores-Palacios and García-Franco 2006, Wolf *et al.* 2009). Trees may develop more suitable microhabitats for epiphytes when they grow larger, such as larger and more horizontal branches, crevices, and forks. Bark may also get more weathered when trees get older, and some tree species may develop a generally more rough and rugged bark structure when they get larger. In addition, more suitable substratum may be provided by relatively stress-tolerant colonist epiphytes, and associated fauna such as ants (Benzing 1990).

6.1.4 Epiphyte presence on rubber trees and other trees

As rubber is the dominant tree species in jungle rubber agroforests, the suitability of the rubber tree as a host tree for epiphytes is a major factor in the suitability of the jungle rubber land use type as a whole for the conservation of epiphytes.

Rubber trees appear to be suitable host trees for epiphytic ferns in Malaysia (Madison 1979), despite being an introduced species from South America. Since large areas in the Malaysian region are planted with rubber trees, as much as three million hectares in Indonesia in 1997 (Ministry of Forestry and Estate Crops 1998), it is relevant to compare the suitability of *Hevea brasiliensis* as a host tree for Malaysian epiphytic ferns to that of other locally present, and mostly native, host trees.

Human actions may make rubber trees more suitable as host trees, e.g. by damaging the bark trough tapping, or, in rubber plantations, by topping young rubber trees to increase rubber production, thus providing a niche for epiphytes in the first fork.

6.1.5 Land use and management practices

The vegetation structure in rubber plantations and jungle rubber agroforests is different from that in primary forest (Figures 4.4 and 4.5 in Chapter 4), potentially affecting the growing conditions for epiphytes in terms of microclimate and available light.

Land use may also affect the growth rate of trees. Young trees growing in full light after slash-and-burn may grow faster than young trees growing in the understorey or in a gap in primary forest. In addition, management practices by farmers and plantation managers will actively promote the growth rate of desired trees in rubber production systems. In jungle rubber, those practices consist of weeding in the first few years after planting, and slashing and ring-barking to remove competing unwanted trees during the preproductive phase of the rubber. In rubber plantations, management includes the use of pesticides and fertilizers in addition to weeding and slashing of understorey vegetation. Consequently, trees in the same DBH-class may actually be older in primary forest than in rubber plantations and jungle rubber agroforests.

6.1.6 Outline of chapter

In this chapter, I first describe the epiphyte habitat in this study, in terms of the distribution of trees in DBH classes in the three land use types (primary forest, jungle rubber and rubber plantations), and the change in abundance of rubber trees and other trees with increasing age of jungle rubber agroforests. I then describe habitat use by epiphytic ferns in the land use types by comparing the percentage of trees in plots that carry (fertile) epiphytic ferns between land use types. The importance of tree size, tree type and land use type, and interactions of those factors, for the establishment and reproduction of epiphytic ferns is analysed by logistic regression. Finally, the contribution of rubber production systems to the conservation of epiphytic ferns is assessed based on the combined results of the habitat description and the regression models, and limiting factors are identified.

6.2 Method

6.2.1 Study area

The study was carried out in the peneplain area of Jambi province, a slightly undulating to flat area of about 200 by 150 km in the centre of Sumatra, Indonesia. Study plots were located in non-flooding areas at elevations ranging from 40 to 150 meters above sea level. Soils were predominantly well-drained, acid oxisols with low fertility (Wahyunto *et al.* 1990). For sampling locations see Figure 3.1 of Chapter 3. Annual rainfall in the Jambi peneplain is about 3000 mm per year. On average, there are 7 to 8 wet months (>200 mm rainfall/month) per year, and no months with less than 100 mm of rainfall. Rainfall distribution is of the equatorial type with the driest months from May to September (see Figure 4.1 in Chapter 4). Yearly average minimum and maximum temperatures are 22.5 °C and 31.4 °C, respectively.

6.2.2 Plot characteristics

Plots measuring 40 × 40 m (0.16 ha) were established in three land use types: rubber plantations (17 plots), jungle rubber (23 plots), and primary forest (10 plots). All rubber plots were productive and regularly tapped. The age of the rubber plantation plots ranged from 5 to 19 years old, while the age of the jungle rubber plots ranged from 9 to 74 years old. In the analyses describing the epiphyte habitat and comparing percentages of trees with (fertile) epiphytic ferns (sections 6.3.1 and 6.3.2), the 23 jungle rubber plots were split into young jungle rubber (10 plots, age ranging from 9 to 26 years) and old jungle rubber (13 plots, age ranging from 32 to 74 years). The resulting four groups of plots (rubber plantations, young jungle rubber, old jungle rubber, and primary forest) are referred to as land use groups.

For the establishment of most of the jungle rubber agroforests, all previous vegetation was cleared by slash-and-burn, while in only 3 agroforests some large trees survived. Those were left standing because the farmer had to cut down primary forest without the use of a chainsaw. Some trees were harvested for timber from 39% of the agroforests, while non-timber forest products were harvested from all jungle rubber agroforests. Rubber plantations were all established after complete slash-and-burn of the previous vegetation except for one occasion where a farmer spared a valuable durian fruit tree (*Durio zibethinus* Murr.) from the old rubber agroforest that he was replanting. Plantations supplied no timber, and only a limited number of non-timber forest products was harvested from rubber plantations. All jungle rubber agroforests were privately owned. Of the rubber plantations, 12 were privately owned and 5 were owned by a company. In Jambi province, farmers and plantation managers usually do not actively remove epiphytes from rubber trees.

6.2.3 Data collection

Only trees of at least 10 cm DBH that had their stem within the plot boundaries were considered. Trees were assigned to one of three DBH classes: 10–20 cm DBH, 20–40 cm DBH, or > 40 cm DBH. In one young jungle rubber plot, trees were not assigned to DBH classes.

A total of 3983 trees were checked for the presence of epiphytes. Trees were first checked using binoculars and a telescope, then all trees that had epiphytes, or on which the presence of epiphytes was uncertain, were climbed using single-rope climbing techniques. On each tree that carried epiphytic ferns, all fern species were sampled, including fertile specimen where present. A specimen was recorded as fertile when spores or indications of spore production were present. This included spore-bearing structures that were just beginning to form, as well as those where the spores had already fallen out. Table 6.1 presents an overview of trees that were checked for epiphytes.

6.2.4 Data analysis

STATISTICAL ANALYSIS

The statistical package SPSS version 11.5 was used to compare land use groups with respect to the distribution of trees over DBH classes, as well as plot-level percentages of trees that carried epiphytic ferns, and plot-level percentages of trees that carried fertile epiphytic ferns. Where data were normally distributed, an Anova or t-test was used, while

Table 6.1 Trees of DBH >10 cm in four land use groups that were checked for the presence of (fertile) epiphytes.

Land use type	# of plots	Sampled area (ha)	Total # of trees	Total # of trees with epiphytic ferns	Total # of trees with fertile epiphytic ferns
primary forest	10	1.60	949	155	50
old jungle rubber	13	2.08	1111	145	23
young jungle rubber	10	1.60	842	126	6
rubber plantations	17	2.72	1081	204	4
total	50	8.00	3983	630	83

a nonparametric test (Kruskal Wallis test) was used in cases where data were not normally distributed. I used regression analysis in SigmaPlot software version 8.0 to analyse the relation between the number of rubber trees and other trees in plots and the age of plots, for jungle rubber and rubber plantation plots.

For the logistic regression models analysing the presence of (fertile) epiphytic ferns at the level of individual trees, a nested approach was used since the occurrence of trees with epiphytic ferns within plots was not independent.

LOGISTIC REGRESSION MODELS

Two logistic regression models were made for estimating the probability of occurrence of epiphytic ferns and fertile (spore-bearing) epiphytic ferns on rubber trees and other trees in three size classes (DBH-classes) in rubber plantations, jungle rubber agroforests and primary forest. Data input for both models consisted of records for 3983 trees.

Models were based on logistic regression with extra-binomial variation, second-order linearization and penalized quasi-likelihood estimates, using 'MLwiN' version 1.10 software (Rasbash *et al.* 2000, www.cmm.bristol.ac.uk). Multilevel methods were used to account for possible dependency of cases within plots.

One model was made for estimating the probability of occurrence of epiphytic ferns on trees, with the dependent variable being the presence (1) or absence (0) of at least one epiphytic fern on a tree; variable EPIPHYTS. Another model was made for the occurrence of fertile epiphytic ferns on trees, with the dependent variable being the presence (1) or absence (0) of at least one epiphytic fern with spores or indications of spore production on a tree; variable FERTILES.

The independent variables were the same for both models:
- type of tree: rubber tree or other tree; variable TREETYPE (T)
- land use type in which the tree is standing: primary forest (pf), jungle rubber (jr), rubber plantation (pl); variable LANDUSE (L)
- tree diameter: DBH classes small (10–20 cm), medium (20–40 cm), and large (> 40 cm); variable DBHCLASS (D)

Reference class for TREETYPE was 'other', for LANDUSE 'jungle rubber', and for DBHCLASS 'small'.

TAKING DIFFERENCES IN TREE DENSITY INTO ACCOUNT

The mean number of trees of DBH > 10 cm per plot was significantly different between land use groups (Anova, $F = 7.337$, $df = 3$, $P < 0.001$); the mean was 95 for primary forest plots (N = 10), 85 for old jungle rubber plots (32–74 years old, N = 13), 84 for young jungle rubber plots (9–26 years old, N = 10), and 64 for rubber plantation plots (N = 17). The mean number of trees of DBH > 10 cm per plot was significantly lower in rubber plantation plots than in primary forest plots ($P = 0.001$), old jungle rubber plots ($P = 0.011$), and young jungle rubber plots ($P = 0.034$) (Tukey HSD post-hoc test). Density of trees of DBH > 10 cm per hectare was calculated as 593 trees/ha for primary forest (1.6 ha), 534 trees/ha for old jungle rubber (2.08 ha), 526 trees/ha for young jungle rubber (1.6 ha), and 397 trees/ha for rubber plantations (2.72 ha). To take lower tree density in rubber plantations into account, I compared land use groups in section 6.3.2 on the basis of per-plot percentages of trees that had (fertile) epiphytic ferns.

Within land use groups, I found no significant relation between the percentage of trees of DBH > 10 cm that carried epiphytic ferns and the total number of trees of DBH > 10 cm in a plot for any of the four land use groups (regression analyses), so the effect of tree density on the occurrence of epiphytic ferns was not further studied.

6.3 Results

6.3.1 Description of the epiphyte habitat: tree size and tree type in land use types

TREE SIZE IN LAND USE GROUPS: DISTRIBUTION OF TREES OVER DBH CLASSES

Figure 6.1 shows, for each DBH class, the average number of trees in plots in the four land use groups. The number of trees of 10–20 cm DBH per plot was normally distributed in all land use groups, and means were not significantly different between land use groups (Anova, $F = 1.624$, $df = 3$, $P = 0.197$). The number of trees of 20–40 cm DBH per plot was normally distributed in primary forest and old jungle rubber only. In young jungle rubber, 56% of the plots had no trees of 20–40 cm DBH, while in rubber plantations 47% of the plots had no trees of 20–40 cm DBH, resulting in skewed distributions with median values of 0 and 2, respectively. The number of trees of 20–40 cm DBH per plot was significantly different between land use groups (Kruskal Wallis test, Chi-square = 10.470, $df = 3$, $P = 0.015$). The number of trees of > 40 cm DBH per plot was normally distributed in primary forest and in old jungle rubber, and their means were not significantly different (t-test, $F = 0.154$, $P = 0.698$). None of the plots in young jungle rubber and rubber plantations had trees larger than 40 cm DBH.

The number of trees per hectare was calculated per DBH class for the four land use groups (see Table 6.2).

NUMBER OF RUBBER TREES AND OTHER TREES

On average, jungle rubber plots consisted for 41% of rubber trees. Although the total number of trees of DBH > 10 cm did not significantly change with the age of jungle rubber

Table 6.2 Calculated number of trees per hectare in DBH classes, for primary forest (1.6 ha), old jungle rubber (2.08 ha), young jungle rubber (1.44 ha), and rubber plantations (2.72 ha). For young jungle rubber, DBH data were available for only 9 of the 10 plots.

Trees / ha	10 – 20 cm	20 – 40 cm	> 40 cm
primary forest	376	134	83
old jungle rubber	347	133	54
young jungle rubber	453	63	0
rubber plantations	325	73	0

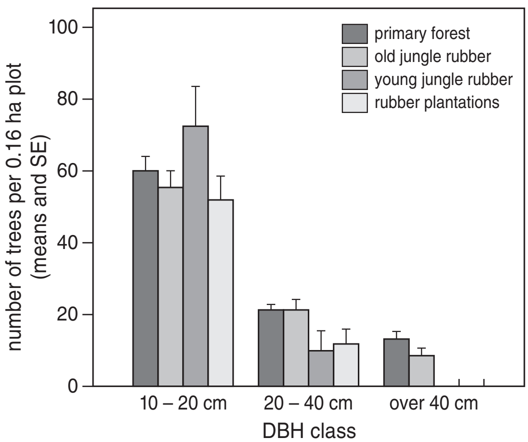


Figure 6.1 Number of trees per plot in DBH classes (means and their standard errors) in four land use groups: primary forest (10 plots), old jungle rubber (13 plots), young jungle rubber (9 plots), and rubber plantations (17 plots).

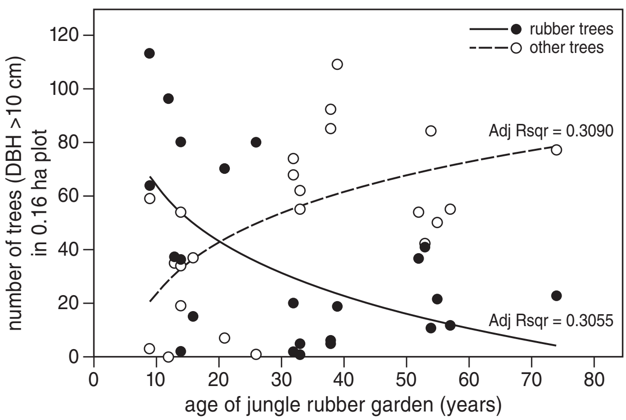


Figure 6.2 Number of rubber trees and other trees of DBH >10 cm in jungle rubber plots of different age.

(regression analysis, P = 0.931), the balance between rubber trees and other trees did change with age. The number of rubber trees significantly decreased with (the natural logarithm of) age (P = 0.0037, Adj R^2 = 0.31) while the number of other trees significantly increased with (the natural logarithm of) age (P = 0.0035, Adj R^2 = 0.31) in jungle rubber agroforests, see Figure 6.2. The number of rubber trees decreased as they suffered from damage caused by tapping and were susceptible to fungal diseases, termites and other pests.

Rubber plantations were usually monocultures when part of large estates or their associated (transmigration) projects, while they had very few other trees when owned by private farmers outside estate areas. On average, rubber plantation plots consisted for 98% of rubber trees.

In rubber plantations, the total number of trees of DBH > 10 cm did not significantly change with the age of the plantation (regression analysis, P = 0.198), and no significant relations were found between the number of rubber trees and the natural logarithm of age (P = 0.2474) and the number of other trees and the natural logarithm of age (P = 0.0605).

6.3.2 Occurrence of epiphytic ferns and fertile epiphytic ferns in land use groups

All primary forest and old jungle rubber plots had trees that carried epiphytic ferns, and per-plot percentages of trees that carried epiphytic ferns were normally distributed in both land use groups. In young jungle rubber, 30% of the plots had no trees that carried epiphytic ferns, while in rubber plantations 47% of the plots had no trees that carried epiphytic ferns. In those two land use groups, the per-plot percentages of trees that carried epiphytic ferns had a skewed distribution.

Median values for the percentages of trees that carried (fertile) epiphytic ferns in plots in the four land use groups are shown in Table 6.3. No significant difference in plot-level percentages of trees that carried epiphytic ferns was found between land use groups (Kruskal Wallis test, Chi-square = 3.246, df = 3, P = 0.355; Median test gave similar result).

All primary forest plots had trees that carried fertile epiphytic ferns, and per-plot percentages of trees that carried fertile epiphytic ferns were normally distributed. In old jungle rubber, 23% of the plots had no trees that carried fertile epiphytic ferns, while in young jungle rubber, 80% of the plots had no trees that carried fertile epiphytic ferns. In rubber plantations, 82% of the plots had no trees that carried fertile epiphytic ferns. In those three land use groups, the per-plot percentages of trees that carried fertile epiphytic ferns had a skewed distribution. Plot-level percentages of trees that carried fertile epiphytic ferns were significantly different between land use groups (Kruskal Wallis test, Chi-square = 26.377, df = 3, P = 0.000; Median test gave similar result).

Table 6.3 Plot-level percentages of trees that carried (fertile) epiphytic ferns, by land use group. Median values for all land use groups; means and their standard errors for normally distributed data only.

	% trees with epiphytic ferns			% trees with fertile epiphytic ferns		
	median	**mean**	**SE**	**median**	**mean**	**SE**
primary forest	14.57	15.79	2.399	4.47	5.01	0.893
old jungle rubber	10.99	13.33	2.014	1.21	-	-
young jungle rubber	6.01	-	-	0	-	-
rubber plantations	3.77	-	-	0	-	-

6.3.3 *Modeling the probability of occurrence of epiphytic ferns and fertile epiphytic ferns on trees*

PRESENCE OF EPIPHYTIC FERNS RELATED TO LAND USE TYPE, TREE DIAMETER CLASS AND TREE TYPE (RUBBER TREES VERSUS OTHER TREES)

Model 1: MODEL FOR THE OCCURRENCE OF EPIPHYTIC FERNS ON TREES
Multilevel analysis (trees within plots) was applied to account for the fact that occurrences of epiphytic ferns on trees within plots were not independent (analysis in 'MLwiN', $chi^2 = 18.12$, 1 df). The model was started with the three independent variables and their 2- and 3-way interactions:

T + L + D + T*L + T*D + L*D + T*L*D.

After subsequent removal of each non-significant interaction, the remaining model consisted of the main factors plus one significant interaction:

T + L + D + pf*medium.

DBH class (D) was very significant with $P << 0.00001$, while the interaction pf*medium (land use 'primary forest' and DBH class '20–40 cm') was significant with $P = 0.008$. Tree type (T) was not significant at the 5% level ($P = 0.089$), but was retained in the model because of its relevance for the study. Land use (L) was not significant as a main effect, but since the significant interaction term had a land use component, the main effect needed to be retained in the model. Coefficients and their standard errors are shown in Table 6.4, as well as the derived odds ratios, which were calculated as EXP(coefficient).

The odds for a medium-sized tree (DBH 20–40 cm) to carry epiphytic ferns were more than three times those for a small tree (DBH 10–20 cm), while the odds for a large tree (DBH > 40 cm) to carry epiphytic ferns were almost six times those for a small tree. The effect of medium-sized trees carrying epiphytic ferns more often than small trees was significantly smaller in primary forest than in jungle rubber.

Table 6.4 Coefficients with their standard errors, and odds ratios, of the model for the occurrence of epiphytic ferns on trees.

Factor	Coefficient	SE (coeff.)	Significance	Odds ratio
tree type	0.325	0.191	n.s.	1.38
pf	0.612	0.628	n.s.	1.84
pl	-0.467	0.577	n.s.	0.63
medium	1.198	0.149	$P << 10^{-5}$	3.31
large	1.768	0.171	$P << 10^{-5}$	5.86
pf*medium	-0.682	0.259	$P = 0.008$	0.51

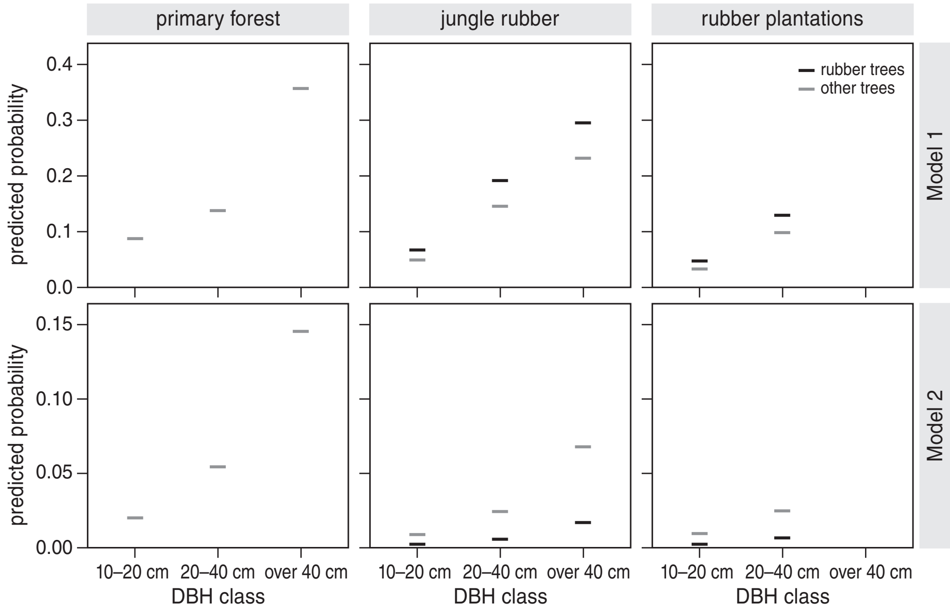


Figure 6.3 Predicted probabilities for the occurrence of epiphytic ferns (Model 1) and fertile epiphytic ferns (Model 2) on trees in Jambi province, Sumatra.

Table 6.5 Predicted probabilities for the occurrence of epiphytic ferns on rubber trees and other trees of different DBH class in three land use types, based on the results of Model 1.

Land use		Primary forest	Jungle rubber		Rubber plantation	
Tree type		**Other trees**	**Rubber trees**	**Other trees**	**Rubber trees**	**Other trees**
DBH	10–20	0.087	0.067	0.049	0.045	0.031
class	20–40	0.138	0.191	0.146	0.129	0.097
(cm)	>40	0.358	0.295	0.232	-	-

While odds ratios were calculated to give the odds related to a particular factor as compared to the reference class, predicted probabilities were calculated for combinations of factors. The predicted probabilities for the occurrence of epiphytic ferns on rubber trees and other trees of different DBH class in three land use types are presented in Figure 6.3 and Table 6.5. The results clearly show the importance of tree size (DBH class) for the occurrence of epiphytic ferns in each land use type.

PRESENCE OF FERTILE EPIPHYTIC FERNS RELATED TO LAND USE TYPE, TREE DIAMETER CLASS AND TREE TYPE (RUBBER TREES VERSUS OTHER TREES)

Model 2: MODEL FOR THE OCCURRENCE OF FERTILE EPIPHYTIC FERNS ON TREES
Multilevel analysis (trees within plots) was applied to account for the possibility that occurrences of fertile epiphytic ferns on trees within plots were not independent (analysis in 'MLwiN', $chi^2 = 3.385$, 1 df), although the dependency effect was much smaller than for the data in the previous model.

Due to missing combinations of factors in the data, the largest model with which the analysis could be started consisted of:

T + L + D + pf*medium + pf*large + pl*medium.

The interactions were non-significant, and were removed. Land use (L) was overall not significant because pl was not different from jr ($P = 0.99$), so pl was removed from the model and became part of the reference class (pl+jr). The final model consisted of:

T + pf + D

which were all significant factors. DBH class (D) was very significant with $P << 0.00001$, tree type (T) was significant with $P = 0.0013$, and land use (pf versus pl+jr) was significant with $P = 0.024$. Coefficients and their standard errors are shown in Table 6.6, as well as the derived odds ratios, which were calculated as EXP(coefficient).

The odds for a medium-sized tree (DBH 20–40 cm) to carry fertile epiphytic ferns were almost three times those for a small tree (DBH 10–20 cm), while the odds for a large tree (DBH > 40 cm) to carry fertile epiphytic ferns were more than eight times those for a small tree. The coefficient for tree type was negative, which means that the odds for a rubber tree to carry fertile epiphytic ferns were lower than for other trees.

The odds for trees in primary forest to carry fertile epiphytic ferns were more than twice those for trees in rubber plantations and jungle rubber. The predicted probabilities for the occurrence of fertile epiphytic ferns on rubber trees and other trees of different DBH class in three land use types are shown in Figure 6.3 and Table 6.7. The results show

Table 6.6 Coefficients with their standard errors, and odds ratios, of the model for the occurrence of fertile epiphytic ferns on trees.

Factor	Coefficient	SE (coeff.)	Significance	Odds ratio
tree type	-1.470	0.458	$P = 0.0013$	0.23
pf	0.841	0.374	$P = 0.024$	2.32
medium	1.040	0.274	$P << 10\text{-}5$	2.83
large	2.113	0.274	$P << 10\text{-}5$	8.27

the importance of tree size (DBH class) for the occurrence of fertile epiphytic ferns in each land use type, as well as relatively high predicted probabilities for primary forest, and relatively low predicted probabilities for rubber trees.

Table 6.7 Predicted probabilities for the occurrence of fertile epiphytic ferns on rubber trees and other trees of different DBH class in three land use types, based on the results of Model 2.

Land use		**Primary forest**	**Jungle rubber**		**Rubber plantation**	
Tree type		**Other trees**	**Rubber trees**	**Other trees**	**Rubber trees**	**Other trees**
DBH	10-20	0.020	0.002	0.009	0.002	0.009
class	20-40	0.055	0.006	0.024	0.006	0.025
(cm)	> 40	0.145	0.016	0.068	-	-

6.4 Conclusions

6.4.1 Conclusions from the logistic regression models

In model 1, the model for the occurrence of epiphytic ferns on trees, the factors land use type (L) and tree type (T) were not significant as main effects. This means that according to the model it did not matter for the colonization by epiphytic ferns whether the tree was a rubber tree or another species of tree, and whether the tree was growing in a rubber plantation, a jungle rubber agroforest or a primary forest. The most important significant factor found in the model was DBH class, or the size of the tree. Larger trees were colonized by epiphytic ferns more often than smaller trees. Both the medium size class (20–40 cm DBH) and the large size class (> 40 cm DBH) were significant as main effects, with the large size class having a higher odds ratio than the medium size class. A significant interaction was found between the primary forest land use type and the 20–40 cm DBH size class. Trees in this size class in primary forest were less often colonized by epiphytic ferns than trees in the same size class in jungle rubber. In other words, if primary forest is regarded as the natural or reference situation, it means that trees in the 20–40 cm DBH size class in jungle rubber and rubber plantations were colonized by epiphytic ferns more often than trees in the same size class in primary forest.

In model 2, the model for the occurrence of fertile epiphytic ferns on trees, the factors tree type (T) and DBH class (D) were both significant as main effects. Rubber trees had fertile epiphytic ferns less often than other trees. With regard to tree size, the pattern was similar to that for model 1, with larger trees having fertile epiphytic ferns more often than smaller trees. Large trees (> 40 cm DBH) in model 2 had the largest odds ratio (8.27) of any of the factors in the models, indicating an important role for large trees in the reproduction of epiphytic ferns. With regard to land use type (L), primary forest (pf) was a significant factor when compared to a reference class of jungle rubber and rubber plantation land use types taken together. Trees in primary forest carried fertile epiphytic ferns more often than trees in the other land use types.

6.4.2 Contribution of land use types to the conservation of epiphytic ferns

Colonization by epiphytic ferns did not seem to constitute a limiting factor in the possible contribution of rubber production systems to the conservation of epiphytic ferns. In non-parametric testing, overall colonization of trees by epiphytic ferns was not significantly different between land use groups. However, the shape of the distribution of per-plot percentages of trees that carried epiphytic ferns was rather different between land use groups. In young jungle rubber and in rubber plantations, some plots had no trees with epiphytic ferns, while in other plots the percentage of trees that carried epiphytic ferns was high.

Reproduction by epiphytic ferns was significantly lower in jungle rubber and rubber plantations than in primary forest, limiting the contribution of rubber production systems to the conservation of epiphytic ferns.

6.5 Discussion

Given the scarcity of large trees in rubber production systems, and the importance of large trees as host trees for epiphytes, I expected lower colonization by epiphytic ferns in jungle rubber and rubber plantations than in primary forest. I did find that about one-third of the young jungle rubber plots and half of the rubber plantation plots had no trees that carried epiphytes, and that tree size was the main factor for the presence of epiphytic ferns in trees in this study. However, the significantly higher colonization of medium-sized trees (20–40 cm DBH) in jungle rubber and rubber plantations as compared to the same size class in primary forest seemed to offset the scarcity of large trees ($>$ 40 cm DBH) in these systems to some extent. A possible explanation might be the difference in illumination of tree crowns of trees in the 20–40 cm DBH class. In rubber production systems, crowns of trees in the 20–40 cm DBH class were predominantly in the uppermost canopy layer, receiving more light than the same size class in primary forest where trees in the $>$ 40 cm DBH size class formed the upper canopy. Colonization of rubber trees seemed slightly higher than colonization of other trees, but this was not a significant effect.

While colonization by epiphytic ferns was comparable between land use groups overall, reproduction was significantly different between land use groups. Tree size was again the main factor for the occurrence of fertile epiphytic ferns on trees, and primary forest had more large trees than the other land use types. Rubber trees carried fertile epiphytic ferns less often than other trees. This may be due to the fact that ferns need time to grow and form spores, whereas fast-growing rubber trees were probably younger than other trees in their DBH class. Rubber trees rarely get very old because of tapping damage, and are often removed to be used as firewood when latex production stops. In old jungle rubber agroforests, some of the productive rubber trees are second generation trees, either from spontaneous seedlings or interplanted by the farmer in an existing agroforest. Finally, trees in primary forest carried fertile epiphytic ferns more often than trees in the other land use types, in all size classes. This may also be a time effect, with trees in primary forest probably being older (slower growing) than trees in the same DBH class in rubber production systems.

For reproduction of epiphytic ferns, the length of the slash-and-burn cycle in jungle rubber systems appears to be a critical limitation, as it determines the availability of large old trees. The gradual replacement of rubber trees by other trees with increasing age of jungle rubber agroforests forms a clear trade-off between conservation and production, as it increases the contribution to the conservation of epiphytic ferns, but decreases production for the farmer. A similar trade-off occurs with the removal of a few large trees for domestic uses during the lifetime of the jungle rubber agroforest, a practice that may be on the increase as availability of wood from other sources declines.

Acknowledgements

Many thanks to Eric Gardette, who kindly shared his experience in climbing techniques and epiphyte research, and provided invaluable advice on climbing equipment purchase and handling. He also directed me to a dedicated and experienced tree climber, Mr. Isron Wah Yudhi, who assisted by Mr. Didi did an excellent job collecting specimen for this research. Thanks to ICRAF, especially to Tom Tomich for providing a budget for climbing equipment and to Dennis Garrity for providing a great herbarium room at the Bogor office.

Many thanks to Cas Kruitwagen of the Centre for Biostatistics, Utrecht University, for carrying out the analyses in MLwiN software, and for his patience in explaining the procedures and results.

References

Benavides, Ana-Maria, Jan H. D. Wolf and Joost F. Duivenvoorden, 2006. Recovery and succession of epiphytes in upper Amazonian fallows. Journal of Tropical Ecology 22 (6), 705-717.

Benzing D.H., 1990. Vascular epiphytes. General biology and related biota. Cambridge University Press, Cambridge, UK.

Beukema H., Danielsen F., Vincent G., Hardiwinoto S., Van Andel J., 2007. Plant and bird diversity in rubber agroforests in the lowlands of Sumatra, Indonesia. Agroforestry Systems 70, 217-242.

Dunn R. R., 2000. Bromeliad communities in isolated trees and three successional stages of an andean cloud forest in Ecuador. Selbyana 21 (1/2), 137-143.

Flores-Palacios A., García-Franco J., 2006. The relationship between tree size and epiphyte species richness: testing four different hypotheses. J Biogeogr 33, 323-330.

Gouyon A., De Foresta H., Levang P., 1993. Does 'jungle rubber' deserve its name? An analysis of rubber agroforestry systems in southeast Sumatra. Agroforest Syst 22, 181-206.

Hietz P., 2005. Conservation of Vascular Epiphyte Diversity in Mexican Coffee Plantations. Conservation Biology 19 (2), 391–399.

Johansson D., 1974. Ecology of vascular epiphytes in West African rain forest. Acta Phytogeographica Suecica 59. Uppsala, Sweden.

Madison M., 1979. Distribution of epiphytes in a rubber plantation in Sarawak. Selbyana 5(2), 207-213.

Ministry of Forestry and Estate Crops, Department of Estate Crops, 1998. Statistics of Estate Crops of Indonesia – Rubber. Ministry of Forestry and Estate Crops, Jakarta, Indonesia.

Rasbash J., Browne W., Goldstein H., Yang M., Plewis I., Healy M., Woodhouse G., Draper D., Langford I., Lewis T., 2000. A user's guide to MLwiN. Version 2.1d (July 2002) for use with MLwiN 1.10. Centre for Multilevel Modelling, Institute of Education, University of London. Available at www.cmm.bristol.ac.uk.

Wahyunto, Subardja D., Puksi D.S., Rochman A., Paidi R., Wahyu W.M., Hidayat A., Dai J., 1990. Explanatory booklet of the land unit and soil map of the Muara Bungo sheet (0914), Sumatra, scale 1:250.000. Centre for Soil and Agroclimate Research, Bogor, Indonesia.

Werner S., 1999. The impact of management practices on species richness within productive rubber agroforests of Indonesia. In: Sist P., Sabogal C., Byron Y. (eds) Management of secondary and logged-over forests in Indonesia. Selected proceedings of an international workshop, Bogor, Indonesia, 17-19 November 1997. CIFOR, Bogor, Indonesia, pp. 33-44.

Wolf, Jan H.D., 2005. The response of epiphytes to anthropogenic disturbance of pine-oak forests in the highlands of Chiapas, Mexico. Forest Ecology and Management 212 (1–3), 376–393.

Wolf, Jan H. D., S. Robbert Gradstein and Nalini M. Nadkarni, 2009. A protocol for sampling vascular epiphyte richness and abundance. Journal of Tropical Ecology 25 (2), 107-121.

Chapter 7

Synthesis

Hendrien Beukema

In this chapter, I reflect on the research questions as presented in Chapter 1, and summarize and reflect on the major results from my research (Chapters 2–6). I give some perspectives on biodiversity conservation in jungle rubber and on the use of pteridophytes as indicators for this purpose, and conclude by outlining three possible scenarios for the future of jungle rubber, and a recommendation for future biodiversity research.

7.1 Justification of research questions

This thesis addresses the question whether the agroforestry system known as jungle rubber can play a role in biodiversity conservation.
The research questions were:

1. What and how much biodiversity is present in jungle rubber, as compared to lowland forest and to monoculture plantations?
2. How can this be assessed and evaluated?
3. What are the limitations of jungle rubber in contributing to biodiversity conservation?
4. Is jungle rubber itself a sustainable land use?

7.1.1 What and how much biodiversity in jungle rubber?

The first question involves a comparison across three land use types, but from a policy perspective it primarily refers to management options with regard to rubber cultivation: low management jungle rubber versus highly managed rubber plantations. I have compared the biodiversity in these two land use types with that in old growth forest, for the sake of simplicity often called primary forest.

The old growth lowland forest in the research area was not so much a land use option as it was a remnant of a previously forested landscape that in the past experienced a very low intensity of use by a very small population. Currently, almost all 'forest land' in the Jambi lowlands is cultivated, or allocated for cultivation. Old growth forest served as a reference point, both in the rationale for this research, as well as in the assessment and evaluation of biodiversity found in the rubber cultivation types.

The assumption that lowland rain forest, situated in one of the world's biodiversity hotspot areas, has a value to humanity, and that Indonesia as a country recognizes this value, has motivated the effort to assess whether the jungle rubber system could function as a refuge for at least a part of Indonesia's biodiversity. While there is general agreement that lowland rainforest biodiversity is valuable, this value is highly dependent on international, national, and local policy agendas, and has to compete with value assigned to other policy priorities such as poverty reduction and economic development. With regard to conservation versus conversion of the easily accessible lowland forests of the Jambi peneplain, the latter has clearly dominated in the past decades (Ekadinata and Vincent 2011).

Jungle rubber on the other hand was identified as a potentially multifunctional land use integrating ecological and economical benefits (Tomich *et al.* 1998), though both seemingly at sub-optimal levels. The research question of 'How much biodiversity in jungle rubber?' came up (Gouyon *et al.* 1993) in the context of a rapidly changing landscape in the early 1990s, when signs of massive conversion of rain forest to monoculture plantations started to be visible in the Jambi lowlands. It is in this context that biodiversity in jungle rubber and rubber plantations needed urgently be compared to that of the original old growth forest.

It is clear that as a vegetation type jungle rubber cannot be expected to resemble old growth forest, due to its woody species composition (planted *Hevea* combined with preferred wild and planted tree species) and the limited age and size of the trees. Rubber has only been planted in Jambi since 1904, and the oldest jungle rubber stands found in Jambi are less than a hundred years old. Thus in terms of forest structure, one can not realistically expect more than a resemblance to late successional forest. Within those constraints though, the question whether species typically found in old growth forest could also be found in jungle rubber, and to what extent, was a feasible and adequate research question.

7.1.2 How was biodiversity assessed?

With regard to the method of answering this question, the choice was made to collect new vegetation data in the field, and to identify and compile existing datasets that the new data could be compared to. New field data was collected on the abundance of terrestrial and epiphytic pteridophyte species, as well as on presence/absence of palms (including rattans), lianas, and epiphytic orchids in the aforementioned three land use types. Existing datasets for comparison included a small dataset on vascular plants, and larger datasets on birds and trees (see Chapter 5).

Research on terrestrial pteridophytes focused on comparing species richness across land use types using species-area curves, as well as on indicator species. For comparing species richness, terrestrial pteridophytes were classified as 'forest species' and 'non-forest species' based on the literature. In addition, (groups of) indicator species were derived by using species abundance models to analyse abundance in relation to the age of jungle rubber or rubber plantations.

Research on epiphytic pteridophytes focused on comparing species richness across land use types using species-area curves, as well as on the occurrence and fertility status of epiphytic pteriophytes on different-sized *Hevea* trees and other trees across land use types.

Comparison of the pteridophyte data to existing datasets was done by comparing species richness patterns in land use types using species-area curves. For the bird data, species were classified as 'forest species' and 'non-forest species'.

7.1.3 What limits biodiversity conservation in jungle rubber?

For the biodiversity research, the two factors that were expected to have the greatest impact on the development of forest-like vegetation associated with rubber were management by the farmer, and age of the rubber plot.

The original research plan called for a range of management intensities to be sampled, but in the field it became clear that the majority of farmers tended to choose between two strategies: rubber plantations that were high-input and highly managed, versus jungle rubber that was low-input and minimally managed. Although there was variation among rubber plots in each group with regard to the details of the management regime, there was a clear distinction in management level between the groups.

Plots were selected for the biodiversity research in such a way that different ages were represented, so successional trends in the vegetation could be studied, and the importance of tree size for epiphytic pteridophyte populations could be investigated.

Interviews and literature study made clear that the management level and age of rubber plots are themselves the outcomes of farmers' decisions with regard to the rubber plots and other land they own. Factors involved in these decisions are farmers' capital and labor resources, land use options and preferences, technical and ecological knowledge, as well as outside influences. These include commodity prices, large scale plantation projects, alternative income sources, village-level development projects, market prices for secondary products such as timber and fruits, and the availability of improved planting material.

7.1.4 Is jungle rubber itself a sustainable land use?

In a landscape where lowland forests have been largely converted to highly managed plantations, the question whether jungle rubber itself is expected to be a sustainable land use is crucial if jungle rubber is to play a role as a refuge for forest biodiversity. Sustainability depends primarily on the choice by individual farmers to keep cultivating rubber in a low-input, low-management manner. The outcome of individual choices for a plantation-style monoculture (of rubber, oil palm, or fast-growing trees) or a jungle rubber agroforest will eventually determine the importance in terms of area of jungle rubber in the landscape. In addition, there will likely be changes in the nature of the jungle rubber system, such as shortening of the life cycle through shortening of pre-productive and post-productive periods. Vegetation dynamics in jungle rubber may also change as a result of land use trends in the area. For instance, cultivating jungle rubber on previously cultivated land rather than on forest land may increase weed problems and the need for investment in herbicides, while the lack of nearby forest may lead to poor regeneration of useful woody species in jungle rubber.

7.2 Biodiversity

The focus of my research was on the diversity and the indicator values of terrestrial and epiphytic pteridophytes, but the results have also been compared with diversity of trees and birds, thus getting an impression of the representativeness of pteridophyte diversity for comparing the land use types under investigation.

7.2.1 Terrestrial pteridophytes

The overall number of terrestrial pteridophyte species registered inside plots was 65. Average plot level species richness (11 species) was not significantly different amongst the three land use types.

To assess forest habitat quality in rubber production systems as compared to primary forest, terrestrial pteridophyte species were grouped as ‘forest species’ or ‘non-forest species’. Species–area curves based on ‘forest species’ alone showed that the understorey environment of jungle rubber supports intermediate numbers of ‘forest species’ and is much more forest-like than that of rubber plantations, but less than primary forest. Pteridophyte species richness alone, without *a priori* ecological knowledge of the species involved, did not provide this information.

7.2.2 Epiphytic pteridophytes

The overall number of epiphytic pteridophyte species registered inside the plots was 30. Comparison of species-area curves showed that richness in epiphytic pteridophyte species was lower in jungle rubber than in forest, and slightly lower again in rubber plantations.

Logistic regression was used to assess the importance of land use, tree size, and tree type for colonization and reproduction of epiphytic ferns. Primary (old growth) forest and old jungle rubber had more large trees than young jungle rubber and rubber plantations. In rubber plantations, 98% of trees were rubber trees, whereas on average only 41% of trees in jungle rubber were rubber trees. Rubber trees were gradually replaced by other trees with increasing age of jungle rubber.

The occurrence and fertility status of ferns on rubber trees and other trees in three size classes (Diameter at Breast Height 10–20 cm, 20–40 cm, > 40 cm) were recorded. A total of 3983 trees were checked for epiphytic ferns, of which 949 trees were in primary forest (1.6 ha), 1953 in jungle rubber gardens (3.68 ha), and 1081 in rubber plantations (2.72 ha).

For the occurrence of epiphytic ferns on trees, only tree size was significant as a main effect. Larger trees were colonized by epiphytic ferns more often than smaller trees. For the occurrence of fertile epiphytic ferns on trees, both tree type and tree size were significant as main effects. Rubber trees had fertile epiphytic ferns less often than other trees. Tree size was the most important significant factor, with larger trees having fertile epiphytic ferns more often than smaller trees. Large trees (> 40 cm DBH) had the largest odds ratio (8.27) of any of the factors in the models, indicating an important role for large trees in the reproduction of epiphytic ferns.

Primary forest was a significant factor when compared to a reference class of jungle rubber and rubber plantation land use types taken together, indicating that trees in primary forest carried fertile epiphytic ferns more often than trees in the other land use types. It appears that rubber plantations contribute little to the conservation of epiphytic ferns, whereas jungle rubber contributes more as stands get older and have more large, non-rubber trees.

7.2.3 Comparison of diversity of several groups

Plant and bird diversity in the jungle rubber agroforestry system was compared to that in primary forest and rubber plantations by integrating new and existing data. Species accumulation curves were compiled for terrestrial and epiphytic pteridophytes, trees and birds, and for subsets of ‘forest species’ of terrestrial pteridophytes and birds. Comparing jungle rubber and primary forest, groups differed in relative species richness patterns. Species richness in jungle rubber was slightly higher (terrestrial pteridophytes), similar (birds) or lower (epiphytic pteridophytes, trees, vascular plants as a whole) than in primary forest. For subsets of 'forest species' of terrestrial pteridophytes and birds, species richness in jungle rubber was lower than in primary forest. For all groups, species richness in jungle rubber was generally higher than in rubber plantations.

7.3 Terrestrial pteridophytes as indicators of forest-like conditions

My first approach was to explore the available literature to identify habitat preferences of the pteridophyte species under investigation. This allowed me to create a list of 'forest' and 'non-forest' species. Based on field data, species were also classified into six groups according to apparent ecological similarity with respect to presence and abundance in plots of different land use types and ages, and both classifications were compared. Finally, I proposed a number of pteridophyte species that – either or not clustered – can be used as indicators of forest disturbance and/or forest regeneration. Here I summarise the results.

7.3.1 Forest and non-forest species

Pteridophytes as a group contained enough species that differ in habitat requirements to be used as an indicator group. Important environmental factors affecting life in the understorey of a tropical lowland rain forest that change with disturbance are light conditions (quantity and spectrum) and microclimate (moisture and temperature regime).

Species classified as 'forest species' were all species that require shade or deep shade plus species that prefer light shade and grow in forest. Classified as 'non-forest species' were all species of open and open/light shade conditions plus species that prefer light shade and habitats other than forest (roadsides, forest edges, plantations etc.). This species grouping allowed me to assess which part of the total terrestrial pteridophyte diversity in each land use type was made up by species requiring forest-like conditions (see section 7.2.1). Assuming that the bigger the share of those 'forest species', the more forest-like the understorey environment would tend to be, the species grouping facilitated the assessment of forest habitat quality of the understorey in jungle rubber and rubber plantations.

The grouping also facilitated comparison of terrestrial pteridophyte diversity with diversity of other groups (see section 7.2.3) such as epiphytic pteridophytes and trees (assumed to largely consist of 'forest species') as well as 'forest species' of birds. Though only a few major groups could be compared, the comparison with groups inhabiting different niches in the forest extended the assessment of forest-like conditions beyond the understorey to the entire forest environment, and gave a more complete picture of diversity levels in jungle rubber than terrestrial pteridophyte data alone.

7.3.2 Species grouping evaluated

The 65 species of terrestrial pteridophytes in the dataset were classified in five groups according to apparent ecological similarity with respect to presence and abundance in plots of different land use types and ages, while a sixth group was formed containing those species that were only found in primary forest. This grouping based on field data was compared to the previous species classification of 'forest species' and 'non-forest species' derived from literature. The two classifications were generally in agreement, indicating that an *a priori* classification of terrestrial pteridophyte species into two groups based on light requirements may be used to interpret data in biodiversity and succession studies at the community level.

7.3.3 Indicator species

For a subset of 29 species that were common in the dataset, frequencies of individual species were modeled with respect to plot age to detect successional patterns. The patterns identified by modeling helped characterize individual species as either transient or climax species in secondary forest succession in the study area.

Species and species groups that showed clear abundance patterns in relation to disturbance and forest age were subsequently selected as potential indicators of forest disturbance and/or forest regeneration. It should be noted that some environments such as flooded banks and edges of forest streams as well as micro-environments such as steep earth walls were not included in the sampling.

Blechnum orientale, *Microlepia speluncae*, *Nephrolepis biserrata*, *Dicranopteris linearis* var. *linearis*, *Asplenium pellucidum*, *Lygodium microphyllum* and *Lygodium flexuosum* indicate highly to moderately disturbed early successional situations. Those species are all common in the Malaysian region and are easy to recognise. In chronosequence studies, decrease in abundance and disappearance of these species with age may indicate forest regeneration.

Nephrolepis biserrata may be particularly suitable to track restoration of forest after fire or slash-and-burn. This species was present over the full length of the successional gradients in rubber plantations and jungle rubber, as well as in forest after fire, with different abundance patterns. It was found to be very abundant in the most disturbed situations, such as burned forest in the first years after forest fire, newly planted fields after slash-and-burn, rubber plantations, and very young jungle rubber. Its abundance decreased rapidly in jungle rubber between 21 and 26 years of age, but the species remained present with intermediate abundance in all but a few jungle rubber plots. *N. biserrata* was rarely found in primary forest, and when it was present it was represented by a single small individual. This species can be expected to gradually disappear in older secondary forest.

Selaginella willdenowii and *Dicranopteris linearis* var. *subpectinata* are also easily recognisable species, and indicative of moderate disturbance associated with secondary forest succession.

Presence of *Taenitis blechnoides*, *Tectaria singaporeana*, *Lindsaea doryphora*, *Mesophlebion chlamydophorum*, *Tectaria barberi*, and *Schizaea digitata* is indicative of (the restoration of) a forest environment. The number of such species found in disturbed forest samples relative to the number found in undisturbed forest samples could be a useful measure of forest restoration or of forest quality. The same can be said of a group of species that in this study was found only in forest.

Higher abundances of *Taenitis blechnoides* may point to relatively less disturbed situations when samples from different land use types, such as plantations and agroforests, are compared.

7.4 Choice of the study area and generalization of the results

The rubber growing zone in the lowlands of Jambi province extends to the west into the foothills of the Barisan mountain range, where the boundary of a national park is located. In terms of practical applicability of the outcomes of this research, a choice for this area at the forest margin as the study area would seem justified. The area was relatively remote as compared to areas closer to the main provincial roads and the provincial capital of Jambi, and there was much jungle rubber in the area, at relatively close distance to the forest. Previous ecological research was carried out in this area, located around the district capital of Rantau Pandan (Gouyon *et al.* 1993), and it has become an important focus area for research into land use options and policies (Murdiyarso *et al.* 2002).

However, the forest margin area is characterized by steep slopes and more variation in soil type than the central area of the Jambi lowlands. From a methodological point of view, sampling in this area would have introduced much variation in terrain, including variation in soil type, slope steepness, and altitude, and associated variation in microclimate such as moisture levels. Especially variation in moisture levels would have been a concern, as some pteridophyte species that are known to prefer wet conditions would have been indicating terrain features rather than land use.

While recognizing that there may have been some direct effects of soil heterogeneity on species composition in the plots, the choice for the central area of the Jambi lowlands, where terrain features were more uniform and slopes were not steep, has probably afforded a better view on differences caused by land use and age of the plots, which were the focus of the research. Conclusions of the research in terms of relative differences in species richness of the land use types, and the importance of the age of jungle rubber, can probably be applied to the forest margin areas as well. I observed that jungle rubber was cultivated in much the same way in the Rantau Pandan area as it was in the study area, with a similar development of the secondary forest component. However, absolute species richness numbers in the forest margin area may be slightly higher due to a more varied terrain.

While this study was performed in the peneplain of Jambi province in Sumatra, results may apply to the larger area of the uplands of the central peneplains of Sumatra, which have similar soil and climate conditions, as described by Scholz (1983). In addition, most of the pteridophyte species mentioned in this study as indicators of disturbance are widely distributed geographically, and may therefore be useful indicators in other lowland forest areas in the Malaysian region, such as Peninsular Malaysia and the island of Borneo.

7.5 Constraints to biodiversity in a multifunctional land use

The role that rubber agroforests can play in biodiversity conservation is limited by the fact that it is a production system that has to be profitable for the farmer. Management practices such as planting, weeding and selection as well as the length of the planting cycle affect vegetation composition and recolonisation by wild species. Even when jungle rubber is not regularly cleaned, farmers generally support desired tree species, either wild or planted, by protecting seedlings, while unwanted tree species are actively removed from gardens by slashing and ring-barking.

Werner (1999) compared the vegetation of secondary forest, cleaned rubber gardens and unmanaged rubber gardens in Kalimantan, and concluded that "regular selective cleaning practices are the major reason for differences in botanical composition and biodiversity of rubber gardens and unmanaged fallow". Rubber gardens in her study had lower numbers of tree species than unmanaged secondary forests. She also found that the difference in number of species between secondary forest and rubber gardens was more pronounced for tree species than for other plant groups.

In Singapore, Turner *et al.* (1997) found that the mean tree species number per plot in a diverse type of approximately 100-year-old secondary forest was about 60% of that in primary forest, which is much higher than the relative tree species richness in jungle rubber found in this study (around 30%). Length of the planting cycle is a major limitation for biodiversity conservation in jungle rubber.

Jungle rubber is replanted when the number of rubber trees and latex production become too low to be profitable, on average after about 40 years. Late-successional trees may not reproduce in such a short time, and plant groups such as epiphytes that depend on later successional stages of forest may not have had enough time to establish and reproduce. We found that several epiphytic pteridophyte species observed in forest were never found in jungle rubber. Those species may be limited to much older secondary forest or to primary forest.

Epiphytic orchids are known to colonise secondary forest more slowly than epiphytic pteridophytes (Johansson 1974). We observed that epiphytic orchids were present in fewer jungle rubber plots than epiphytic pteridophytes, with lower abundance, and were never found flowering or fruiting in jungle rubber.

Whether or not the moderate diversity levels of 'forest species' of plants and birds are seen as important to conservation of lowland rain forest biodiversity depends on the larger context of land use change and forest conservation in the area. These different points of view will be discussed in the next sections.

7.6 Perspectives

7.6.1 On the use of pteridophytes as indicator species

When species richness is compared over a range of land use types, different patterns emerge for different groups. The conclusion reached by Lawton *et al.* (1998) that "attempts to assess the impacts of tropical forest modification and clearance using changes in the species richness of one or a limited number of indicator taxa to predict changes in richness of other taxa may be highly misleading" seems justified. Results from this research for vascular plants and birds point in the same direction with regard to species richness.

Terrestrial pteridophytes were found to be slightly more species rich in jungle rubber than in primary forest, whereas species richness of epiphytic pteridophytes and trees was much lower in jungle rubber than in primary forest. Species richness of vascular plants as a whole was lower in jungle rubber than in primary forest, but this could indeed not be predicted from the relative species richness of one or a limited number of subgroups. For birds no real difference in total species richness between jungle rubber and primary forest was found within the relatively short sampling time. I agree with Lawton *et al.* (1998) that changes in overall species richness of individual taxa or subgroups as such are not informative enough to study impacts of forest conversion.

However, the findings of this research suggest that when ecological characteristics of species are taken into account, relative species richness of 'forest species' may be a useful indicator of the biodiversity conservation value of the jungle rubber land use type. As this value tends to be overestimated by including species that are not usually associated with primary forest, there is a clear need for ecological information at the species level to allow for species classifications that are relevant to conservation.

In bird studies, this ecological information is usually available and applied to the results. Danielsen and Heegaard (2000) found a reduction of specialised insectivore birds of the midcanopy and understorey, and of woodpeckers, in jungle rubber as compared to forest; they also found that birds are affected by regular presence of rubber tappers and by hunting, reflected in a reduction of pheasants.

Several studies in tropical America and Africa found high bird species richness in agroforests as compared to nearby forests, but altered composition with regard to ecological groups (Tejeda- Cruz and Sutherland 2004, Cockle *et al.* 2005, Waltert *et al.* 2005, Faria *et al.* 2006).

In vegetation studies, the practice of taking ecological characteristics of species into account when interpreting results is common in well-researched ecosystems with limited species diversity, but not very common in highly diverse tropical rain forest ecosystems.

Pteridophytes proved in this study to be a relatively well-described group suitable to indicate local environmental conditions. Because the spores are wind dispersed, their occurrence is not limited by presence of other organisms required for most seed dispersal or pollination. However, this characteristic of pteridophytes makes the group less suitable to represent biodiversity of other taxa. Hunting pressure and habitat fragmentation will affect some taxa more than others. Pteridophytes alone would probably provide us with a too optimistic view on biodiversity in jungle rubber.

7.6.2 On the role of jungle rubber in biodiversity conservation

Since many lowland rain forest species are threatened, and unlikely to find a suitable habitat in jungle rubber or other disturbed forest types, priority should be given to conservation of remaining primary forest patches (see also Gibson *et al.* 2011). In addition, jungle rubber can contribute to conservation of lowland forest remnants as well as higher altitude forests by providing buffer zones and connectivity (Ekadinata and Vincent 2011), and as a refuge for part of the forest species.

Although species conservation in jungle rubber is limited by management practices and by a slash-and-burn cycle for replanting that limits its age, this forest-like land use does support species diversity in an impoverished landscape increasingly dominated by monoculture plantations.

The very low richness values for 'forest species' of plants and birds in rubber plantations and the absence of whole groups of organisms from rubber plantations as shown in this thesis are clear indicators of the impoverished landscape that is being created by the current large scale conversion process.

7.6.3 On sustainability of jungle rubber

Jungle rubber is still being planted and grown, though a shorter life cycle can be expected for this rubber. Otherwise, the basic characteristics of jungle rubber do not seem to have changed much since its introduction. The strategy of minimizing inputs is still a sensible option for some farmers, if only for part of their rubber holdings. At the landscape level however there seems to be a change away from jungle rubber systems and towards plantation style cultivation (Ekadinata and Vincent 2011), making jungle rubber a less common feature in the landscape.

Historically, most jungle rubber has been planted on land that was previously old growth forest. Apart from socio-economic reasons such as land rights and accommodating a growing population, the reason farmers preferred to establish jungle rubber on previously uncultivated land was the much smaller risk of weed problems. Future jungle rubber however will necessarily be planted more and more on land that has previously been cultivated, which may cause weed problems to interfere with the low-input, low-management strategy that characterizes the system.

Another effect of the scarcity of old growth forest may be diminished source populations of forest species, at larger distances. When jungle rubber is planted after slash-and-burn, wild species establish themselves anew in the rubber plot. But first they have to be able to reach the plot in order to do so. Reduction of vertebrate fauna through hunting may have a larger negative effect on tree diversity than previously expected (Harrison *et al.* 2013). This sourcing problem may affect both the future biodiversity levels in jungle rubber, as well as the attractiveness of the system if the spontaneous establishment of desired species such as fruit and timber trees were to be affected.

Diversification of land use in the Jambi lowlands has led to more land use options for farmers. These include monoculture plantations of rubber, oil palm, and fast-growing trees that can be financially more rewarding for farmers, but do not provide the ecosystem services and multifunctionality that jungle rubber gardens provide. Some farmers have converted, or will convert, all or some of their jungle rubber to other, more intensively managed land uses, while for others the jungle rubber system may remain an attractive option.

Efforts to make jungle rubber systems more productive may on the one hand make them more attractive for farmers, while on the other hand these efforts themselves may reduce biodiversity in those systems, for instance by concentrating on a few profitable woody species rather than a diverse mixture.

Other efforts to encourage farmers to maintain jungle rubber focus on the ecological services provided by the jungle rubber system, including nutrition, water management, carbon storage, and biodiversity conservation, and look for ways to reward farmers for these services.

7.7 Outlook

In this section, I present three alternative scenarios for the future of jungle rubber, incorporating both economic and ecological aspects. To conclude this chapter, I provide a recommendation for future biodiversity research.

7.7.1 Scenario 1: Strong reduction in jungle rubber area

While the end of jungle rubber has been predicted at several points in time throughout its history, the unprecedented economic growth in Asia may finally have changed the equation in Sumatra in favor of monoculture production for good. Continued economic and population growth have created a stronger demand and higher prices for commodities such as rubber, palm oil, and wood for the pulp and paper industry.

Not only is price the strongest incentive for intensification, the increased demand also puts pressure on land availability, making jungle rubber even less attractive as compared to monocultures. In other words, in this scenario there is no interest, no space, and no economic rationale anymore to keep the natural forest component in the jungle rubber system. Rice, fruits, vegetables, and medicine are bought rather than integrated in the cultivation system, and firewood is replaced by fossil fuels.

This trend reinforces itself as profits made in monoculture cultivation attract migrants, putting further pressure on land availability, expanding infrastructure, and stimulating encroachment into ‘protected’ forest areas. The resulting landscape will be dominated by monoculture plantations with very little jungle rubber, and a reduced area of ‘protected’ forest with actual borders higher up the mountain.

7.7.2 Scenario 2: Gradual erosion of jungle rubber area and character

The trend in land use change for Bungo district in Jambi province, described by Ekadinata and Vincent (2011) for the 1973–2005 period, has two important components with regard to jungle rubber: a reduction in jungle rubber area (from 15% to 11%), and a shift in location of jungle rubber across the landscape. Areas that were covered by rubber agroforests in 1973 had mostly been converted to monoculture plantations by 2005, while rubber agroforests present in 2005 mostly occupied areas that were covered by natural forest in 1973.

If this trend continues, the eventual result will be a smaller jungle rubber area located in areas that are the least accessible and least desirable for investment in monoculture plantations. It will also eventually put an end to the practice of converting forest to jungle rubber, as there won't be forest left to convert. Rubber agroforests replanted on formerly cultivated land may be different in character, for instance if there are more weed problems the farmer has to deal with, management may become more intensive.

There may be other factors stimulating a more intensive management, such as high rubber prices and land pressure, making a higher labor input for weeding and a higher density of rubber trees economical. The extensive management character that provided so much room for nature may erode under those pressures, resulting in simplified rubber agroforests with higher rubber densities and fewer other trees and secondary vegetation. Complexity in terms of vegetation stratification and species diversity may give way to simplified systems that are still agroforests, but may contribute much less to biodiversity conservation than jungle rubber. Areas with much rubber agroforest may become a mix of jungle rubber and simplified rubber agroforests.

7.7.3 Scenario 3: Jungle rubber is valued as a multifunctional land use

Efforts to value jungle rubber in a broader perspective focus on finding what works in the domain of payments for ecological services (PES) (Van Noordwijk *et al.* 2012). Although new PES approaches may not be able to secure large areas of jungle rubber, they will provide very important models for the current transition phase of localized rapid rural development and regional climate and food security adaptations that many tropical areas are currently going through.

Functionality of the landscape rather than biodiversity conservation is emphasized in this phase (Akiefnawati *et al.* 2010). But in the future, biodiversity may feature higher on the list of priorities of local communities, and restoration efforts may find remaining jungle rubber an interesting starting point. The idea of a refuge implies a temporary state. How well the refuge functions, and for how long, may to some extent depend on the success of local innovations in PES strategies that are currently being developed.

7.7.4 Recommendation for biodiversity research

With respect to biodiversity in jungle rubber agroforests, the question that remains is whether the biodiversity levels that have been assessed in the past will be maintained in a landscape that is now dominated by monoculture plantations, and where remaining (logged) forest and old jungle rubber areas are more fragmented.

Remote sensing based spatial studies on land use change and fragmentation combined with a series of ecological monitoring plots would provide us with insight in the changes taking place. Since tree diversity and regeneration will be crucial to lowland rain forest restoration, monitoring should focus on trees, their dispersal mechanisms, and success of establishment both in jungle rubber agroforests and in forest remnants. The research by Tata (Tata 2008, Tata *et al.* 2008) and Rasnovi (2006) on the diversity of seedling and sapling stages of trees could provide a starting point for a long term monitoring study in Jambi province.

References

Akiefnawati, R., Villamor, G. B., Zulfikar, F., Budisetiawan, I., Mulyoutami, E., Ayat A. and Van Noordwijk, M., 2010. Stewardship agreement to reduce emissions from deforestation and degradation (REDD): case study from Lubuk Beringin's Hutan Desa, Jambi Province, Sumatra, Indonesia. International Forestry Review 12, 349-360.

Ekadinata, A. and G. Vincen, G., 2011. Rubber agroforests in a changing landscape: analysis of land use/cover trajectories in Bungo district, Indonesia. Forests, Trees and Livelihoods 20, 3-14.

Gouyon, A., De Foresta, H., and Levang, P., 1993. Does 'jungle rubber' deserve its name? An analysis of rubber agroforestry systems in southeast Sumatra. Agroforestry Systems 22, 181-206.

Rasnovi, S., 2006. Ekologi regenerasi tumbuhan berkayu pada sistem agroforest karet (Regeneration ecology of woody trees in rubber agroforest systems). Doctoral dissertation. Sekolah Pasca Sarjana, Institut Pertanian Bogor. Bogor, Indonesia.

Tata, M. H. L., 2008. Mycorrhizae on dipterocarps in rubber agroforests (RAF) in Sumatra. Thesis, University of Utrecht.

Tata, H. L., Van Noordwijk, M., and Werger, M., 2008. Trees and regeneration in rubber agroforests and other forest-derived vegetation in Jambi (Sumatra, Indonesia). Journal of Forestry Research 5, 1-20.

Tomich, T. P., Van Noordwijk, M., Vosti, S. and Witcover, J., 1998. Agricultural development with rainforest conservation: methods for seeking best bet alternatives to slash-and-burn, with applications to Brazil and Indonesia. Agricultural Economics 19(1-2), 159-174.

Van Noordwijk, M., Leimona, B., Jindal, R., Villamor, G. B., Vardhan, M., Namirembe, S., Catacutan, D., Kerr, J., Minang, P. A., Tomich, T. P., 2012. Payments for Environmental Services: evolution towards efficient and fair incentives for multifunctional landscapes. Annu. Rev. Environ. Resour. 37, 389-420.

Summary

Introduction

With the disappearance of undisturbed lowland rain forest habitat the question arises whether disturbed habitat maintains some of the characteristics and functions of the original forest, to what extent it can support survival and reproduction of primary rain forest species and how this function is influenced by management practices. This thesis is an assessment of the role of rubber (*Hevea brasiliensis*) agroforests in the conservation of lowland rain forest species in Sumatra. Primary forest and monoculture rubber plantations were included in this study to provide reference systems for biodiversity and rubber production values. The primary forest in this study was old growth forest without visible traces of timber cutting and without known history of logging or shifting cultivation, the only human use being limited collection of non-timber forest products and hunting.

Jungle rubber and rubber plantations

Jungle rubber gardens are low-input rubber agroforests that structurally resemble secondary forest and in which wild species are tolerated by the farmer. In this study, jungle rubber agroforests consisted of a mixture of wild and planted vegetation dominated by rubber trees. These agroforests were usually only weeded for a few years after the rubber was planted. Rubber plantations were mostly monocultures, their vegetation structure and composition mainly determined by plantation management practices such as continued weeding and the use of herbicides.

Length of the slash-and-burn production cycle was, on average, about 20 years for rubber plantations and about 40 years for jungle rubber agroforests. In rubber plantations, 98% of trees were rubber trees, whereas on average only 41% of trees in jungle rubber agroforests were rubber trees. Rubber trees were gradually replaced by other trees with increasing age of jungle rubber agroforests.

Method

The study was carried out in the lowlands of the peneplain area of Jambi province, a slightly undulating to flat area of about 200 by 150 km in the centre of Sumatra, Indonesia. Study plots were located in non-flooding areas at elevations ranging from 40 to 150 meters above sea level. Soils were predominantly well-drained, acid oxisols with low fertility. Annual rainfall was about 3000 mm per year. The original forests of this area are mixed Dipterocarp rain forests.

New data was collected on terrestrial and epiphytic pteridophytes in 11 primary forest plots, 23 productive rubber agroforest plots, and 17 productive rubber plantation plots measuring 40 m × 40 m (0.16 ha/plot). Frequency of terrestrial pteridophyte species was assessed by counting species presence in 16 (10 m × 10 m) subplots in each plot, yielding a frequency score between 0 and 16 for each species in each plot. In addition, data was collected on the number of individuals of pteridophytes in the understorey, vegetation structure, litter layer, soil color, slope steepness and position of the plot on the hill slope. Epiphytic ferns were collected in these plots from trees of at least 10 cm DBH using single-rope climbing techniques. Age of jungle rubber plots varied from 9 to 74 years, while the age of rubber plantation plots was 5–19 years old. Existing data on trees and birds was re-analysed for comparison with the pteridophyte results. Interviews were held to collect information on age and management history of the rubber plots.

Species diversity

Terrestrial pteridophyte species were grouped according to their ecological requirements into ‘forest species’ and ‘non-forest species’. Species-accumulation curves were compiled for terrestrial and epiphytic pteridophytes, trees and birds, and for subsets of ‘forest species’ of terrestrial pteridophytes and birds.

Species richness in jungle rubber was slightly higher (terrestrial pteridophytes), similar (birds) or lower (epiphytic pteridophytes and trees) than in primary forest. For subsets of ‘forest species’ of terrestrial pteridophytes and birds, species richness in jungle rubber was lower than in primary forest. For all groups, species richness in jungle rubber was generally higher than in rubber plantations.

Terrestrial pteridophytes

Terrestrial pteridophyte species can serve as indicators of disturbance or forest quality, as many species show clear habitat differentiation with regard to light conditions and/or humidity. The 65 species of terrestrial pteridophytes in the dataset were classified in five groups according to apparent ecological similarity with respect to presence and abundance in plots of different land use types and ages, while a sixth group was formed containing those species that were only found in primary forest. This grouping based on field data was compared to a previous species classification derived from literature that focused primarily on light requirements of species (‘forest species’ and ‘non-forest species’). The two classifications were generally in agreement. Groups found mostly in rubber plantations and (young) jungle rubber consisted predominantly of species that according to the literature preferred open or lightly shaded conditions. Species found mostly in jungle rubber appeared as an intermediate group, with half of the species preferring open or lightly shaded conditions and the other half preferring more shady conditions. The species that were found mostly in jungle rubber and primary forest all preferred shady conditions. The agreement between the grouping based on field data and the literature-based classification indicated that an *a priori* classification of terrestrial pteridophyte species into two groups based on light requirements may be used to interpret data in biodiversity and succession studies at the community level.

Shade increases with age in both jungle rubber agroforests and rubber plantations.

Therefore, one can expect terrestrial pteridophyte species preferring sunny conditions to be replaced over time by species preferring shady conditions in both land use types. Species composition of terrestrial pteridophytes was studied in the undergrowth of chronosequences of productive jungle rubber agroforests, aged 9 to 74 years old, and productive rubber plantations, aged 5 to 19 years old, while species composition in primary forest served as a reference for the undisturbed situation. Change in species composition with plot age was more pronounced in jungle rubber than in rubber plantations. With increasing age of jungle rubber plots, species found mostly in rubber plantations and (young) jungle rubber – such as *Blechnum orientale*, *Microlepia speluncae*, *Nephrolepis biserrata*, *Stenochlaena palustris*, *Dicranopteris linearis* var. *linearis*, *Asplenium pellucidum*, *Lygodium microphyllum*, *Lygodium flexuosum*, *Christella subpubescens* and *Lygodium salicifolium* – became generally less abundant, especially after about 30 years, when some of these species disappeared altogether. In rubber plantations, some species found usually in jungle rubber and primary forest appeared in older plantations, but with lower abundance than in jungle rubber plots. Older rubber plantations were increasingly dominated by two ground-covering species, namely *Nephrolepis biserrata* and *Stenochlaena palustris*.

Frequencies of individual species were modeled with respect to plot age to detect successional patterns for a subset of 29 species that were common in the dataset. Patterns identified by modeling helped characterize individual species as either transient or climax species in secondary forest succession in the study area.

Epiphytic ferns

To assess the importance, by logistic regression, of land use, tree size, and tree type for colonization and reproduction of epiphytic ferns, the occurrence and fertility status of ferns on rubber trees and other trees in three size classes (DBH 10–20 cm, 20–40 cm, > 40 cm) was recorded. A total of 3983 trees were checked for epiphytic ferns, of which 949 trees were in primary forest (1.6 ha), 1953 in jungle rubber agroforests (3.68 ha), and 1081 in rubber plantations (2.72 ha). The availability of large trees, the suitability of rubber trees as host trees, and habitat differences caused by land use practices were expected to influence habitat suitability.

For the occurrence of epiphytic ferns on trees, only tree size was significant as a main effect. Larger trees were colonized by epiphytic ferns more often than smaller trees. A less important significant interaction indicated that medium sized trees in rubber systems were colonized more often than trees in the same size class in primary forest.

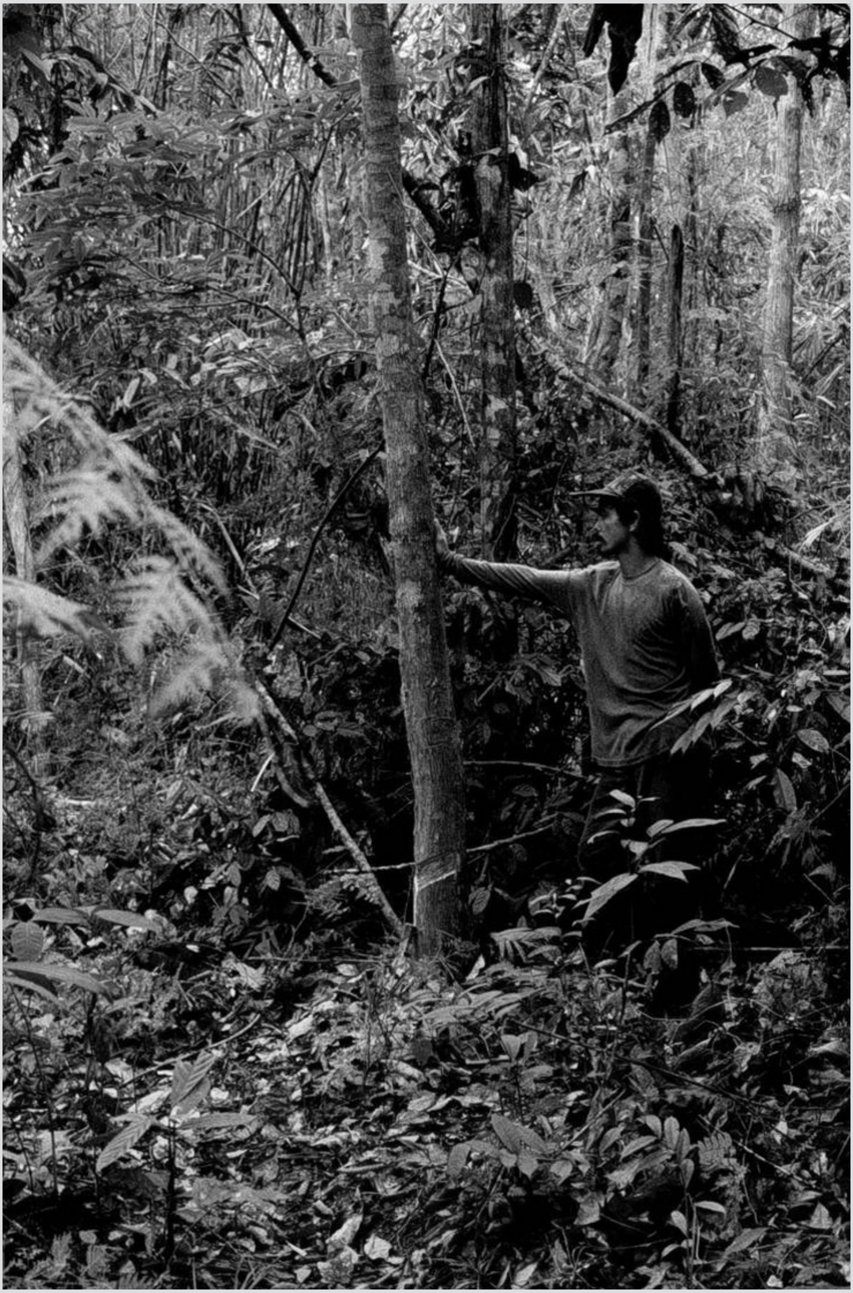
For the occurrence of fertile epiphytic ferns on trees, both tree type and tree size were significant as main effects. Rubber trees had fertile epiphytic ferns less often than other trees. Tree size was the most important significant factor, with larger trees having fertile epiphytic ferns more often than smaller trees. Large trees (> 40 cm DBH) had the largest odds ratio (8.27) of any of the factors in the models, indicating an important role for large trees in the reproduction of epiphytic ferns. Primary forest was a significant factor when compared to a reference class of jungle rubber and rubber plantation land use types taken together, indicating that trees in primary forest carried fertile epiphytic ferns more often than trees in the other land use types.

Conclusions

- The understorey environment of jungle rubber supports intermediate numbers of 'forest species' and is much more forest-like than that of rubber plantations, but less so than primary forest. Species richness alone, without *a priori* ecological knowledge of the species involved, did not provide this information.
- Several species of terrestrial pteridophytes can be used as indicator species for forest disturbance and forest regeneration.
- Although species conservation in jungle rubber is limited by management practices and by a slash-and-burn cycle for replanting of about 40 years, this forest-like land use does support species diversity in an impoverished landscape increasingly dominated by monoculture plantations.
- Rubber plantations contribute little to the conservation of epiphytic ferns, whereas jungle rubber agroforests contribute more as they get older and have more large, non-rubber trees. However, older agroforests also tend to be less productive for the farmer.

Outlook

Sustainability of the jungle rubber land use type depends primarily on the choice by individual farmers to keep cultivating rubber in a low-input, low-management manner. The outcome of individual choices for a plantation-style monoculture (of rubber, oil palm, or fast-growing trees) or a jungle rubber agroforest will eventually determine the importance in terms of area of jungle rubber in the landscape. In addition, there will likely be changes in the nature of the jungle rubber system, such as shortening of the life cycle through shortening of pre-productive and post-productive periods. Vegetation dynamics in jungle rubber may also change as a result of land use trends in the area. For instance, cultivating jungle rubber on previously cultivated land rather than on forest land may increase weed problems and the need for investment in herbicides, while the lack of nearby forest may lead to poor regeneration of useful woody species in jungle rubber. In places where primary forest is still present, priority should be given to conservation of remaining primary forest patches.



Samenvatting

Introductie

Met het verdwijnen van het laaglandregenwoud rijst de vraag of de begroeiing die ervoor in de plaats komt een aantal kenmerken en functies van het oorspronkelijke bos kan behouden. Kan deze begroeiing een bijdrage leveren aan het voortbestaan van soorten uit het regenwoud? En zo ja, hoe wordt deze functie beïnvloed door de manier waarop de begroeiing wordt beheerd? Dit proefschrift is een evaluatie van de rol van *rubber* (*Hevea brasiliensis*) *agroforests* in het behoud van soorten van het laaglandregenwoud in Sumatra. Primair bos en rubberplantages dienden als referentiesystemen voor biodiversiteits- en rubberproductie-waarden.

Jungle rubber en rubber plantages

Jungle rubber tuinen zijn extensieve *rubber agroforests* die qua structuur op secundaire bossen lijken, en waarin wilde soorten door de boer worden getolereerd. De *jungle rubber agroforests* in deze studie hadden zowel wilde als aangeplante soorten, met rubber als dominante boomsoort. Deze *agroforests* werden na het planten van de rubber meestal slechts een paar jaar gewied. De rubberplantages waren meest monoculturen. De vegetatiestructuur en soortensamenstelling van deze plantages werd vooral door het plantagebeheer, zoals voortdurend wieden en het gebruik van herbiciden, bepaald.

De lengte van de *slash-and-burn* productiecyclus was gemiddeld ongeveer 20 jaar voor de rubberplantages en ongeveer 40 jaar voor de *jungle rubber agroforests*. De rubberplantages bestonden voornamelijk uit rubberbomen (98% van de bomen), terwijl het percentage rubberbomen in de *jungle rubber agroforests* gemiddeld slechts 41% was. Met toenemende leeftijd van de *jungle rubber agroforests* werden de rubberbomen geleidelijk vervangen door andere bomen.

Methode

Het veldwerk voor dit onderzoek werd in het laagland van de provincie Jambi uitgevoerd. Dit is een licht golvend tot vlak gebied van ongeveer 200 bij 150 km in het centrum van Sumatra in Indonesië. De proefvlakken lagen in niet-overstromende gebieden op een hoogte van 40 tot 150 meter boven zeeniveau. De bodems waren overwegend goed doorlatende, zure oxisols met een lage vruchtbaarheid. De jaarlijkse neerslag was ongeveer 3000 mm per jaar. De oorspronkelijke bossen van dit gebied zijn gemengde Dipterocarp regenwouden.

Nieuwe gegevens over terrestrische en epifytische pteridofyten werden in 11 proefvlakken in primair bos, 23 proefvlakken in productieve *rubber agroforests*, en 17 proefvlakken in productieve rubberplantages verzameld. De proefvlakken hadden een afmeting van 40 m × 40 m (0,16 ha/proefvlak). Om de frequentie waarmee de verschillende soorten terrestrische pteridofyten in de proefvlakken voorkwamen te bepalen, werd de aanwezigheid van de soorten in 16 subproefvlakken van 10 m × 10 m binnen elk proefvlak genoteerd. Hierdoor werd een frequentiescore tussen 0 en 16 verkregen voor elke soort in elk proefvlak. Daarnaast werden gegevens over het aantal individuen van pteridofyten in de ondergroei, de vegetatiestructuur, de strooisellaag, de bodemkleur, de steilheid van de helling en de positie van het proefvlak op de helling verzameld. Epifytische varens werden met behulp van *single-rope* klimtechnieken uit bomen van minstens 10 cm DBH in dezelfde proefvlakken verzameld. De leeftijd van de *jungle rubber* proefvlakken varieerde van 9 tot 74 jaar, terwijl de leeftijd van de proefvlakken in rubberplantages 5 tot 19 jaar was.

Bestaande gegevens over bomen en vogels werden opnieuw geanalyseerd om deze met de resultaten voor pteridofyten te vergelijken. Interviews werden gehouden om informatie over de leeftijd en beheersgeschiedenis van de rubber proefvlakken te verzamelen.

Soortenrijkdom

Terrestrische pteridofytensoorten werden in twee groepen verdeeld naar ecologische preferentie: 'bossoorten' en 'niet-bossoorten'. Voor terrestrische en epifytische pteridofyten, bomen en vogels, en voor subsets van 'bossoorten' van terrestrische pteridofyten en vogels werden soorten-accumulatiecurves gemaakt.

De soortenrijkdom in *jungle rubber* was in vergelijking met primair bos iets hoger (terrestrische pteridofyten), ongeveer even hoog (vogels) of lager (epifytische pteridofyten en bomen). Voor subsets van 'bossoorten' van terrestrische pteridofyten en vogels was de soortenrijkdom in *jungle rubber* lager dan in primair bos. Voor alle groepen gold dat de soortenrijkdom in *jungle rubber* over het algemeen hoger was dan in rubberplantages.

Terrestrische pteridofyten

Terrestrische pteridofytensoorten kunnen als indicator van verstoring of van boskwaliteit dienen, omdat veel soorten duidelijke verschillen vertonen wat betreft hun preferentie voor zonnige of schaduwrijke condities en/of vochtigheid. De 65 soorten terrestrische pteridofyten in de dataset werden in vijf groepen ingedeeld op basis van ecologische gelijkenis met betrekking tot hun aanwezigheid en abundantie in proefvlakken van verschillende landgebruikstypen en leeftijden, terwijl een zesde groep werd samengesteld uit soorten die alleen in het primaire bos werden gevonden. Deze groepering op basis van veldgegevens werd met een eerdere indeling vergeleken, die ontleend werd aan de literatuur en vooral op de lichtbehoefte van soorten ('bossoorten' en 'niet-bossoorten') gericht was. De twee classificaties kwamen over het algemeen overeen.

De groepen die het meest in rubberplantages en (jonge) *jungle rubber* werden gevonden bestonden voornamelijk uit soorten die volgens de literatuur bij voorkeur in open of licht beschaduwde omstandigheden groeien. Soorten die het meest in *jungle rubber* werden gevonden vormden een tussengroep, waarvan de helft van de soorten de voorkeur aan open of licht beschaduwde omstandigheden gaf en de andere helft aan meer schaduwrijke omstandigheden. De soorten die het meest in *jungle rubber* en primair bos werden gevonden gaven alle de voorkeur aan schaduwrijke omstandigheden. De overeenstemming tussen beide groeperingen, die op basis van veldgegevens en die op basis van de literatuur, gaf aan dat een *a priori* indeling van terrestrische pteridofytensoorten in twee groepen op basis van lichtbehoefte gebruikt kan worden om gegevens in biodiversiteits- en successieonderzoek te interpreteren.

Schaduwrijkheid neemt toe met de leeftijd van zowel *jungle rubber agroforests* als rubberplantages. Daarom kan men verwachten dat in beide landgebruikstypen terrestrische pteridofytensoorten met een voorkeur voor zonnige omstandigheden in de loop der tijd door soorten met een voorkeur voor schaduwrijke omstandigheden worden vervangen. De soortensamenstelling van terrestrische pteridofyten in de ondergroei van productieve *jungle rubber agroforests* van 9 tot 74 jaar oud en productieve rubberplantages van 5 tot 19 jaar oud werd bestudeerd, waarbij de soortensamenstelling in primair bos als referentie voor de ongestoorde situatie diende. De verandering in de soortensamenstelling met de leeftijd van het proefvlak was in *jungle rubber* meer uitgesproken dan in rubberplantages. Met toenemende leeftijd van de *jungle rubber* proefvlakken werden soorten die meestal in rubberplantages en (jonge) *jungle rubber* voorkomen – zoals *Blechnum orientale*, *Microlepia speluncae*, *Nephrolepis biserrata*, *Stenochlaena palustris*, *Dicranopteris linearis* var. *linearis*, *Asplenium pellucidum*, *Lygodium microphyllum*, *Lygodium flexuosum*, *Christella subpubescens* en *Lygodium salicifolium* – over het algemeen minder abundant, vooral na ongeveer 30 jaar, wanneer een aantal van deze soorten helemaal verdween. In oudere rubberplantages verschenen enkele soorten die meestal in *jungle rubber* en primair bos voorkwamen, maar met lagere abundantie dan in de *jungle rubber* proefvlakken. Rubberplantages werden naarmate ze ouder werden steeds meer door twee bodembedekkende soorten, namelijk *Nephrolepis biserrata* en *Stenochlaena palustris*, gedomineerd.

Voor een subset van 29 soorten die veel in de dataset voorkwamen werden de frequenties van individuele soorten gemodelleerd met betrekking tot de leeftijd van de proefvlakken. De gevonden patronen hielpen om de individuele soorten als successie- of climaxsoorten in de successie van het secundaire bos in het studiegebied te karakteriseren.

Epifytische varens

Logistische regressie werd gebruikt om het belang van landgebruik, boomgrootte en boomtype voor de kolonisatie en reproductie van epifytische varens te beoordelen. Hiervoor werd de aanwezigheid van epifytische varens, en van epifytische varens met sporen, op rubberbomen en andere bomen in drie grootteklassen (DBH 10–20 cm, 20–40 cm, > 40 cm) geanalyseerd. In totaal werden 3.983 bomen op epifytische varens gecontroleerd, waarvan 949 bomen in primair bos (1,6 ha), 1953 in *jungle rubber agroforests* (3,68 ha), en 1081 in rubberplantages (2,72 ha). De verwachting was dat de beschikbaarheid van grote bomen, de geschiktheid van rubberbomen als gastheer, en habitatverschillen veroorzaakt door het landgebruik invloed op de geschiktheid van de habitat zouden hebben.

Voor de aanwezigheid van epifytische varens op bomen was alleen boomgrootte significant als hoofdeffect. Grotere bomen werden vaker door epifytische varens gekoloniseerd dan kleinere bomen. Een minder belangrijke significante interactie gaf aan dat middelgrote bomen in rubbersystemen vaker gekoloniseerd werden dan bomen in dezelfde grootteklasse in primair bos.

Voor de aanwezigheid van epifytische varens met sporen waren zowel boomtype als boomgrootte significant als hoofdeffect. Rubberbomen hadden minder vaak epifytische varens met sporen dan andere bomen. Boomgrootte was de belangrijkste significante factor, waarbij grotere bomen vaker epifytische varens met sporen hadden dan kleinere bomen. Grote bomen (>40 cm DBH) hadden de grootste *odds ratio* (8,27) van alle factoren in de modellen, wat op een belangrijke rol voor grote bomen in de reproductie van epifytische varens duidt. Primair bos was een significante factor in vergelijking met een referentieklasse van *jungle rubber* en rubberplantages samen, wat aangeeft dat bomen in primair bos vaker epifytische varens met sporen hadden dan bomen in de andere landgebruikstypen.

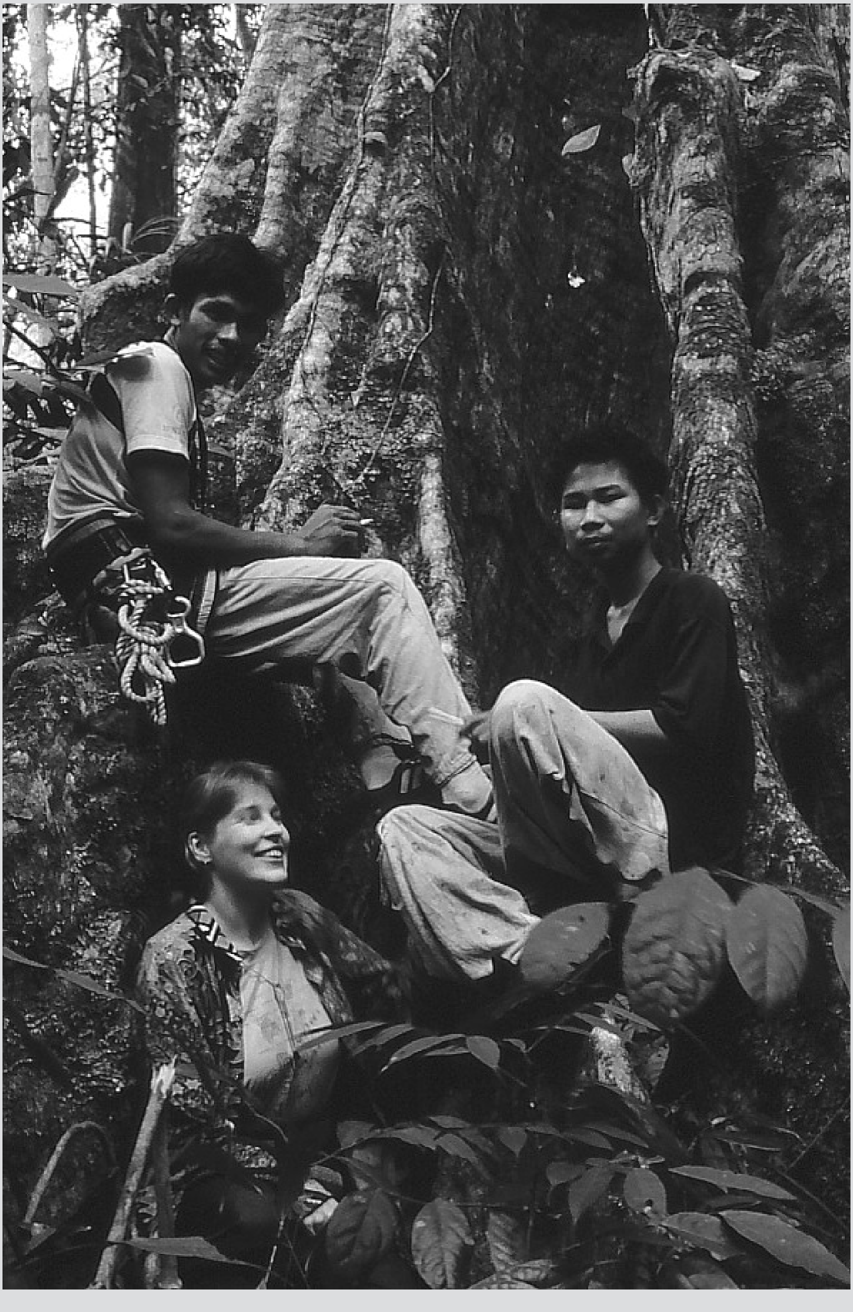
Conclusies

- De omstandigheden in de ondergroei van *jungle rubber* zijn zodanig dat een redelijk aantal 'bossoorten' wordt gevonden, en het milieu is er meer bosachtig dan in rubberplantages, maar minder dan in primair bos. Uit de soortenrijkdom alleen, zonder *a priori* ecologische kennis van de betrokken soorten, zou deze conclusie niet getrokken kunnen worden.
- Verscheidene soorten terrestrische pteridofyten kunnen als indicatorsoorten voor bosverstoring en regeneratie van het bos gebruikt worden.
- Hoewel het behoud van soorten in *jungle rubber* door het beheer en door een herbeplantingscyclus van ongeveer 40 jaar wordt beperkt, draagt dit bosachtige landgebruik bij aan de soortenrijkdom in een verarmd landschap dat steeds meer door monocultuurplantages gedomineerd wordt.
- Rubberplantages dragen weinig bij aan het behoud van epifytische varens, terwijl *jungle rubber agroforests* meer bijdragen naarmate ze ouder worden en meer grote niet-rubber bomen hebben. Wel is het zo dat oudere *agroforests* meestal minder productief voor de boer zijn.

Vooruitzicht

De duurzaamheid van *jungle rubber* als landgebruikstype is vooral afhankelijk van de keuze van individuele boeren om door te gaan met het cultiveren van rubber op deze extensieve manier. De uitkomsten van deze individuele keuzes, hetzij voor monocultuurplantages (van rubber, oliepalm, of snelgroeiende bomen), hetzij voor *jungle rubber agroforests*, zullen uiteindelijk bepalen hoe groot het areaal aan *jungle rubber* in het landschap zal zijn. Bovendien zullen er waarschijnlijk veranderingen in het karakter van het *jungle rubber* systeem optreden, zoals het verkorten van de herbeplantingscyclus door verkorting van de pre- en post-productieve fasen.

De vegetatiedynamiek in *jungle rubber* kan ook veranderen als gevolg van veranderingen in het landgebruik in het onderzoeksgebied. Zo kunnen er meer problemen met onkruid optreden wanneer rubber op eerder gecultiveerd land geplant wordt in plaats van op land waar voorheen alleen bos heeft gestaan. Dit kan investeren in herbiciden noodzakelijk maken. Het ontbreken van nabijgelegen bos kan tot een verminderde regeneratie van nuttige houtige soorten in *jungle rubber agroforests* leiden. Op plaatsen waar primair bos nog aanwezig is, zou het behoud van de resterende bosfragmenten prioriteit moeten krijgen.



Acknowledgements

Acknowledgements

I would like to thank everyone at UNESCO, LIPI, NWO, and ICRAF, who made my research in Indonesia possible. I am much indebted to the Directors and staff of the UNESCO office in Jakarta and the UNESCO Division of Ecological Sciences in Paris, who agreed to let me work at ICRAF as a UNESCO Associate Expert and who were always so friendly and helpful. The idea to work at ICRAF in Bogor came from Prof. Mike Swift, who told me about the 'excellent, dynamic group of researchers' at the 'Alternatives to Slash-and-Burn' Programme at ICRAF's Southeast Asia Regional Office, and kindly helped me transfer there. To the Indonesian Institute of Sciences (LIPI) my sincere thanks for giving me permission to do research in Indonesia. The Netherlands Organisation for Scientific Research (NWO) provided a grant to extend my research in Indonesia, and to write up the results at the University of Groningen as a dissertation in the framework of the NWO/WOTRO programme 'Biodiversity in disturbed ecosystems'.

At ICRAF, I would like to thank Dr. Dennis Garrity for letting me work in his team and for creating such a great workplace, not just for ICRAF staff but for outside researchers as well. I learned a lot from the way the 'Alternatives to Slash-and-Burn' Programme, at the time led by Dr. Tom Tomich and Dr. Meine van Noordwijk, was set up to provide an overall framework for cooperation while allowing researchers from different disciplines to each fill in a piece of the puzzle. I have greatly enjoyed this diversity at ICRAF, where one could look at the same overall questions and study areas from all these different angles through the work of colleagues. 'Context is everything', as Pak Meine would say.

The office staff at ICRAF in Bogor and Muara Bungo was absolutely wonderful, and I owe them many thanks for their help, their endless friendliness and their patience. Ibu Josephine and her team were always there for us, anticipating our every need in Bogor. Ibu Ratna Akiefnawati and the field team in Jambi created a solid and indispensible base in Muara Bungo to come back to after working at research locations in different corners of the province. A place to refuel, play badminton, eat well, and get commented on my sylvan odor (*bau hutan!*) and need for sleep. Many thanks also to Ratna for coordinating a local team who interviewed farmers about new rubber plantings, which became part of Chapter 2.

Many thanks to (now Dr.) Sandy Williams for friendship and moral support in the field. I cherish the memories of first starting my fieldwork in Jambi, when she took such great care of me and introduced me to life in 'her village' Muara Buat. While it rained and rained, Hubert de Foresta took me to see his research sites there despite being soaked, and taught me all about jungle rubber, collecting and preserving plants, and how to deal with leeches. His early work on jungle rubber provided the inspiration and a firm basis for my research, and his support and insights were a great help to me. Eric Gardette helped me more than I can thank him for, introducing me to pteridophyte research and safe climbing techniques, and inviting me to Malaysia where he was working on lianas. I had a chance to see the research forest at Pasoh, as well as the endless monoculture plantations of oil palm and rubber dominating the landscape there.

Thanks to all of the fabulous researchers, Indonesian and international, that I had a chance to meet and work with and who volunteered their time to advise me during my research. The inspiration I got from the work of other researchers was one of the most enjoyable aspects of my work in Bogor. I have learned so much from the interesting and insightful work of Genevieve Michon, Suyanto, Patrice Levang, Daniel Murdiyarso, Sylvia Werner, Gede Wibawa, Yves Laumonier, Deborah Lawrence, Carol Colfer, Franz Gatzweiler, Andy Gillison, Nining Liswanti, Hanna Tuomisto, Arild Angelsen, Suseno Budidarsono, Wil de Jong, Doug Sheil, Leslie Potter, Eric Penot, Laxman Joshi, Quirine Ketterings, Ibu Upik Wasrin, and many others. Thanks to Tropenbos for inviting me to a great workshop in Balikpapan. When I was there, Mark van Nieuwstadt invited me to his remote forest camp at the Sungai Wain research site in East Kalimantan. It was interesting to recognize many of the same pteridophyte species there, and a great opportunity to compare their occurrence in undisturbed and burnt forest, which gave me a better idea of the ecology of different species in relation to disturbance.

Special thanks to my co-authors of Chapter 5: Suryo Hardiwinoto, Finn Danielsen, and Gregoire Vincent. Greg was stationed at ICRAF in Bogor, and I met Prof. Hardiwinoto in the field, in a jungle rubber plot in Jambi, where he was busy collecting tree data with his co-workers from Gadjah Mada University. I met Finn on the other side of the world on Lofoten, a group of islands in the north of Norway, where we both participated in an excellent workshop organized by Arild Angelsen and Genevieve Michon. We quickly found common ground for an article based on our work in jungle rubber. It turned out to be a difficult chapter to write, because we were bringing together different data sets that weren't collected together. Still, working on it was a pleasure because of the good spirit of our cooperation and the many emails coming regularly from Indonesia and Denmark.

The help of experts at the herbarium was vital to clear up problems with identification of specimen. Many thanks to Dr. Dedi Darnaedi and Dr. Irawati of the Bogor Herbarium, and to Dr. Peter Hovenkamp, Dr. Hans Nooteboom and Dr. Marco Roos of the National Herbarium of The Netherlands in Leiden. Specimen collected during my research were deposited at the herbaria in Bogor, Leiden, and Singapore. Thanks also to library staff at the Royal Tropical Institute (KIT) in Amsterdam and the Royal Netherlands Institute of Southeast Asian and Caribbean Studies (KITLV) in Leiden, where I have spent many pleasant hours reading about the history of rubber cultivation.

My research would have been impossible without the help and hospitality of Indonesian people in Jambi province: farmers, villagers, government officials, owners and staff of plantations and logging concessions, and the staff of the ICRAF, UGM, and SEAMEO/BIOTROP research sites. There were no telephones yet outside the towns, so we often turned up unannounced, and were always welcomed and offered a place to stay. Some of my best memories are of those villages where we became a temporary addition to the community. Most of all I am thankful to my local field assistants Yudhi, Didi and Sahyar, who were willing to take the whole endeavor seriously, work hard, and help me understand social situations and local customs. They did this despite the fact that by local standards, the idea of a woman going into the forest to collect ferns for no good reason was hard to understand, to put it mildly. Yudhi did an excellent job of climbing very large trees and collecting epiphytic ferns, as well as dealing with the many unpleasant creatures that tend to live on them.

Finally, I would like to take this opportunity to return to a tradition that I learned to appreciate in Bogor when we lived there, saying *Mohon maaf lahir dan batin* (If I have wronged any of you in any way, I am sincerely sorry).

Dankwoord

Nu dan verder in het Nederlands. Allereerst wil ik natuurlijk mijn directe begeleiders bedanken. Meine zag in mijn eerste resultaten uit het veld aanleiding om mij aan te moedigen er een promotieonderzoek van te maken. We schreven samen de subsidieaanvraag en hoofdstuk 3. Meine, dank je wel voor je steun en begeleiding in Bogor en in het veld, je enthousiasme en goede suggesties, en je rol als copromotor. Ik vond het heel inspirerend om te zien hoe je allerlei samenwerkingsverbanden opzette waarbinnen mensen hun plek konden vinden en een bijdrage konden leveren, daar heb ik veel van geleerd. Ook vind ik het fantastisch om te zien dat het zuidoost-azië kantoor van ICRAF tegenwoordig een vrijwel geheel Aziatische staf heeft; je hebt hierin ongetwijfeld een grote rol gespeeld.

Tweede promotor Marinus wil ik heel hartelijk bedanken voor de prettige samenwerking. Vooral tijdens het schrijfproces heb ik kunnen profiteren van je inzichten en ervaring als redacteur van vele publicaties. Je commentaar op mijn teksten was altijd haarscherp en daardoor bijzonder nuttig en bruikbaar. Je vriendschap en goede samenwerking met Jelte heeft ook veel bijgedragen aan de onderlinge sfeer en daardoor aan het resultaat.

Jelte, waar moet ik beginnen. Bij het begin dan maar, in het noorden van het land. Ooit had je een paar doctoraalstudenten die vastbesloten waren in een oude Peugeot door de woestijn heen naar West-Afrika te rijden om daar hun onderwerp te doen. Mijn goede vriend Wout was daar één van, en zo stond ik op een mooie ochtend ergens op een stoepje in Groningen die gasten uit te zwaaien. Toen ik vervolgens een paar weken later een ansichtkaartje uit Timboektoe kreeg, was ik verkocht. Dat wou ik dus ook. De wereld is groot en mooi, en moet beslist ontdekt worden. Een paar jaar later, ondertussen doctoraalstudent bij jouw vakgroep, kwam ik je daarmee lastig vallen. Tsja, zei je, als je dan echt zo graag naar de tropen wilt, dan kun je maar het beste naar het ITC gaan. En zo ging dat dus, naar Enschede, waar ik me enorm thuisvoelde op het ITC met mensen uit alle windstreken, en waar ook nog eens een heel leuke biologiestudent uit Nijmegen rondliep, een zekere Fred. Van het ITC was het een kleine stap naar een doctoraalonderwerp in Colombia, een baan in Kenia en vervolgens naar Indonesië. Ondanks een goede tijd bij de UvA in de groep van Antoine Cleef, heeft het me eerlijk gezegd altijd een beetje dwarsgezeten dat ik vanwege deze bijzondere route niet bij jouw vakgroep aan de RUG ben afgestudeerd. Dat gaan we nu dus even rechtzetten, en daar ben ik ontzettend blij om. Jelte, je onvoorwaardelijke steun en je vertrouwen heb ik enorm gewaardeerd. Dank je wel voor je hartelijkheid, je tijd en energie, je komst naar Indonesië, en alle positieve en aanmoedigende emails die ik van je kreeg. Ik las je commentaar op mijn stukken met

plezier, je had altijd zulke goede suggesties om de tekst te organiseren en te verbeteren. Nu het boekje klaar is mogen we allebei even terug naar Groningen. Mijn promotie en jouw laatste optreden als promotor, daar gaan we echt even van genieten.

Op het Biologisch Centrum in Haren vond ik heel veel gezelligheid, en ik wil graag iedereen bedanken voor een leuke tijd: Ab, Alma, Anna, Bert, Dries, Emile, Erwin, Esther, Frank, Gerard, Gert Jan, Han, Harold, Jacob, Jan, Joris, Julia, Latzi, Maarten, Manja, Mariska, Michael, Mineke, Nelly, Petra, Rampal, René, Sandra, Stefanie, Yzaak, en alle andere collega's. Koffie drinken met de vakgroep, Sinterklaas, film- en pizza-avondjes, heerlijk met een clubje in de tuin zitten bij een vuurtje, ik heb ervan genoten. Speciaal bedank ik Roos Veeneklaas en Jan van den Burg voor hun hulp met software, Rudy van Diggelen en Ricardo Ibáñez voor hun hulp met de SPSS formules van de HOF curves, Marjan Boertje-Van den Bergh voor allerlei administratieve zaken, de medewerkers van de bibliotheek in Haren voor hun geduld en behulpzaamheid, en Daan Bos voor zijn aanmoedigingen. Applaus langs het parcours is belangrijker dan applaus bij de finish, is mijn ervaring. Renée Bekker had, eerder dan ikzelf, in de gaten dat de beslissing naar Amerika te gaan een mijlpaal was, en vond dat er taart moest komen om het te vieren, iets wat ik achteraf gezien niet had willen missen. Irma Knevel leerde ik in Haren kennen als iemand die hard werken altijd weet te combineren met hartelijkheid en gezelligheid, en die altijd klaar staat voor een ander. Irma, ik ben ontzettend blij dat je paranimf wil zijn bij mijn promotie. Dick Visser wil ik bij deze graag heel hartelijk bedanken voor de prachtige figuren en de layout van dit boekje.

De bijeenkomsten van het NWO/WOTRO programma over biodiversiteit in verstoorde ecosystemen waren een welkome gelegenheid om onderzoekers te ontmoeten die zich met gelijksoortige vragen bezighielden. Dank aan de organisatie, aan alle sprekers voor hun interessante bijdragen, en aan mijn collega-tropengangers Mart Jan Lammertink, Ferry Slik, René Verburg, Karl Eichhorn, en Hans ter Steege voor de inspirerende gesprekken. In Utrecht heeft Cas Kruitwagen me enorm geholpen met de analyse van mijn epifytengegevens voor hoofdstuk 6. Cas zag als statisticus meteen waar de problemen zaten, en wist niet alleen een oplossing, maar kon het ook nog zo uitleggen dat ik er een verhaal van kon maken. Door zijn hulp werd het ineens een heel eenvoudig hoofdstuk om te schrijven.

Mijn vrienden en vriendinnen in Groningen en omgeving wil ik graag bedanken voor de broodnodige afleiding. Na vijf jaar buitenland was het heerlijk om weer in Groningen te zijn, en nog beter om daar samen met jullie van te genieten. En broer Gert: hier heb je dan toch je feestje.

De liefde voor de natuur komt natuurlijk niet uit de lucht vallen. Of het 'nature' of 'nurture' is zullen we maar even in het midden laten, feit is wel dat mijn ouders me van jongs af aan leerden de natuur te waarderen. Op mijn twaalfde verjaardag mocht ik bovendien lid worden van de NJN, en kreeg daarna alle vrijheid om met dat clubje de natuur verder van huis te verkennen. Op te groeien in een huis vol boeken was ook een voorrecht waar ik erg dankbaar voor ben. Bij ons thuis waren er altijd te weinig boekenkasten, nooit te veel boeken. Hierbij dan een kleine toevoeging aan de bibliotheek. Fred en ik hebben een tweede thuis in Nederland, en dat is bij Marlies en Hein, waar de

deur altijd voor ons open staat en waar we zo graag komen. Vanaf onze ITC tijd hebben we al zo veel meegemaakt samen, naar de mooiste plekjes van de wereld gereisd, lastige tijden meegemaakt en weer achter ons gelaten, en altijd plannen genoeg om ons weer verder op te verheugen. Marlies, je bent altijd een grote steun geweest, en het is mede aan jouw luisterend oor te danken dat dit boekje hier nu ligt. Ik ben heel blij dat je er bij bent met de promotie om het samen met ons te vieren, natuurlijk als paranimf, en ik kijk enorm uit naar wat er allemaal nog voor ons ligt. Tot slot, dit boekje is voor Fred, dank je wel voor alles. En nu gaan we weer samen leuke dingen doen.